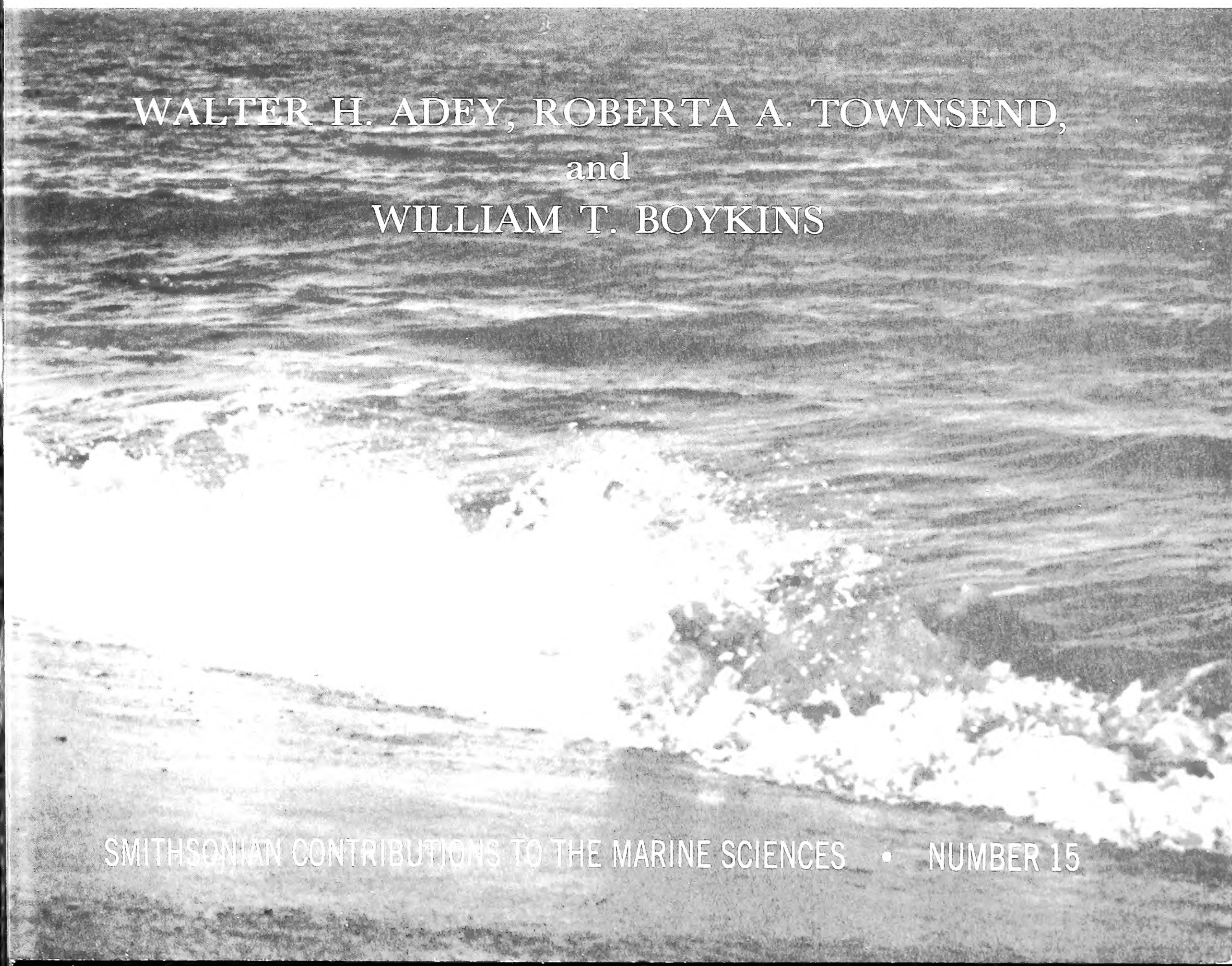
The Crustose Coralline Algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands



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and
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SMITHSONIAN CONTRIBUTIONS TO THE MARINE SCIENCES • NUMBER 15

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The Crustose Coralline Algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands

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ABSTRACT

Adey, Walter H., Roberta A. Townsend, and William T. Boykins. The Crustose Coralline Algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smithsonian Contributions to the Marine Sciences*, number 15, 74 pages, 47 figures, 1982.—Crustose corallines were collected from a wide range of depths (intertidal to about 300 m) throughout the Hawaiian Archipelago. A total of 25 species in 10 genera are recognized on the basis of habit, anatomy, morphology, and ecology, including one new genus and 10 new species. Generic and specific keys for the differentiation of the Hawaiian crustose corallines are also provided.

The ecology of each species, in terms of depth distribution and habitat, is also given, and the potential use of these plants in determining paleoenvironments in the Hawaiian Neogene is discussed.

The Caribbean and Hawaiian crustose coralline floras are briefly compared. The large number of "pair species" and the parallelism in subfamily, generic, and "pair species" ecology indicate that coralline evolution is very slow. The crustose corallines are potentially excellent paleoecological indicators for the Tertiary.

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Contents

The Crustose Coralline Algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands

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Introduction

In the early part of the present century, the marine botanists Howe (1912) and Setchell (1926) stressed the critical importance of crustose corallines as well as other calcareous algae in reef formation. More recently, Littler (1971b, 1973a,b) measured the surface area coverage of organisms at several sites on Oahu. He determined, for the Waikiki fringing reef, that the "crustose coralline algae cover 39% of the reef surface and exceed all other organisms as the major builders and consolidators of reef material" (Littler, 1973a:103), while at 8–28 m, "the deep-water crustose Corallinaceae (38% mean cover) overshadow all other calcareous organisms in terms of standing stock and also seem to have more biological influence than do other limestone producers" (Littler, 1973b:381). Doty (1974) summarized the recent Hawaiian studies of the role of crustose corallines in reef construction.

During the summer of 1965, two holes were cored through the upper Tertiary-Recent limestone cap of Midway Atoll and into the underlying basalt. Ladd, Tracey, and Gross (1967, 1970) and Gross, Milliman, Tracey, and Ladd (1969) concluded that the crustose coralline algae had been the most abundant carbonate building elements in the limestone cap, a situation comparable to that reported for the Recent (Littler, 1971b). At about the same time, a series of borings of a Holocene "algal ridge" and its associated reef flat were begun at the other end of the Hawaiian Archipelago on Hanauma Reef in Oahu (Easton and Olson, 1973). This reef is at present strongly dominated by coralline algae, a condition that seems to have existed during much of the latter half of its 7000-year history.

The present study was conceived to provide the necessary systematic and ecological information needed for the paleoenvironmental interpretation of the crustose coralline algae found in the Midway cores. Previous studies of Pacific corings and exposed limestones (Johnson, 1954, 1958, 1961, 1964) have been of limited value for stratigraphic or paleoecological interpretation because fundamental systematic information has been lacking. In addition, diagnostic characteristics at the specific and even generic levels have been difficult to use in the study of fossil corallines, since the major systematic papers to date are based on a small number of specimens with little information

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about the ecological variation expected within a species.

To rectify this situation, the emphasis of this study has been to delineate the major elements of the Recent crustose coralline algal flora and to describe each species in sufficient detail to allow ecologic treatment of crustose coralline algae by both marine biologists and geologists. As we shall point out, not only are the major coralline genera depth stratified, but to a large extent the depth patterns are evident even at the subfamily level. The following environments of deposition should be differentiable in cores of reefs and limestone caps: quiet lagoon, wave-swept back reef flat, shallow (< 30 m depth) fore reef or algal ridge, mid-depth (30–50 m depths) fore reef, and deep-water banks (50–150 m depths).

This investigation is by no means to be regarded as a comprehensive systematic-ecological study. Although the collection is large, there are a number of taxa represented by only a few specimens. This investigation treats 25 species, using an approach that is a simplified population analysis. The total Holocene crustose coralline flora of the area probably consists of 40–50 species.

Concurrent with the study of the Hawaiian collections, the first author was engaged in an intensive field program in the Caribbean. Considerable emphasis will be placed on the comparison of the floras from these two regions, for example, the marked parallelism in the morphology and ecology of "pair species," and in the spatial ecology of the entire coralline flora at both generic and subfamily levels; however, for purposes of taxonomic identification, the Caribbean species were purposely not considered, because we feel that adequate population data are not available at this time to establish whether or not the many species pairs are identical or evolutionarily divergent. We have kept them in separate taxa. Individual cases are discussed in the species descriptions below.

Tropical provinces of the Atlantic and Pacific have been separated since the Miocene, and genetic interchange for most species prevented. The abundance of "pair species" indicates that crustose coralline algae evolve slowly under tropical conditions. Although this suggests that they would be of little value for tropical stratigraphic correlation, at least for periods of 10–20 million years, it enhances their value for paleoecological investigations. The species composition and ecology presently existing in the Hawaiian chain are probably little different from that which existed throughout the time of deposition of the Midway limestone cap, though additional central Indo-Pacific elements are to be expected in the Miocene, the lower Pliocene, and occasionally in the Pleistocene.

Hawaiian geologists have long considered the reefs in the northwestern part of the Hawaiian Archipelago to be limestone caps on older volcanic islands and that the pattern of evolution of the chain was from the northwest to the southeast. The Midway boring established this pattern and placed it within a time scale of about 20 million years. In terms of plate tectonics, the Pacific plate has been moving WNW over a hot spot in the mantle at a rate of about 10 cm/year during the formation of the Hawaiian chain. A detailed understanding of the ecology of crustose coralline algae, a major component of Hawaiian reefs and banks, could potentially provide considerable insight into the changing patterns of environments occurring while these limestone caps have developed.

ACKNOWLEDGMENTS.—The Latin diagnoses were kindly provided by Dr. Hannah T. Croasdale (Dartmouth College). Field studies for collections were made possible through the support of the National Science Foundation (research grant GA-27343) to the Hawaii Institute of Geophysics of the University of Hawaii. We wish to thank Drs. Isabella Abbott, Michael Borowitzka, Susan Brawley, William Johansen, and James Norris for critically reading the manuscript.

Materials and Methods

The collections for this study were taken by David Child during April and October of 1971

at the locations shown in Figure 1. Transect collections were taken by SCUBA diving from the following zones: intertidal, 0–3, 3–9, 9–15, 15–21, 21–28, 28–37, and 37–46 meters. Dredge collections were taken primarily aboard the University of Hawaii's R/V *Teritu*; those from Nero Bank and Kure taken by the R/V *Agassiz* in 1964 were received from H. Ladd.

Collections by SCUBA were made within each depth zone by taking representative proportions of the different substrate types available to crustose corallines. Because light is also critical in determining coralline populations, an attempt was made to include cryptic areas in the collections in proportion to their occurrence in the sampling area. The SCUBA collections were all made by a project field assistant, David Child, who was familiar with the collecting techniques regularly employed in coralline sampling (see, e.g., Adey, 1971). He was not familiar with the Hawaiian species and would not have unconsciously biased the collections; however, some plants, such as branching species and *Porolithon onkodes* (Heydrich) Foslie, are more conspicuous than others and are perhaps positively biased in our collections. Potential problems of this nature are discussed for each species.

Specimens collected were returned in buckets to a variety of base laboratories and examined alive. Representative samples of each apparent species were live-fixed in Susa's fixative (Suneson, 1937), decalcified with trichloroacetic acid, and prepared for paraffin sectioning by standard techniques (Gray, 1958). Phosphotungstic hematoxylin was used as a stain in all cases (Adey and Johansen, 1972).

Paraffin sectioning of fresh material is critical in the initial study of a poorly known crustose coralline flora; however, once the taxa are delineated in a regional flora, it is not always necessary to paraffin section live material for identification. In many species, surface characteristics, color, and conceptacle dimensions and shape are quite diagnostic for the subfamilies treated herein; however, properly dried and maintained herbarium specimens are essential. Also, microscopic examination of hand sections and fresh vertical fractures of dried crusts are invaluable for taxonomic decisions.

External morphological data such as color, type, and size of branching were taken from dried specimens. The light microscope measurements included in the taxonomic study presented below are based on about 400 sectioned specimens, deposited in the Non-Articulate Coralline Algal Herbarium, National Museum of Natural History, Smithsonian Institution (USNC).

Specimens were prepared for scanning electron microscopy by washing a small piece of crust in distilled water, drying, and mounting on stubs. Carbon coating by evaporation using an E.F.F.A. vacuum evaporator and sputter coating with gold palladium alloy (S.E.M. Laboratory, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA) were done prior to specimen observation with a Cambridge S4-10 scanning electron microscope.

Ecology and the surface aspects of the species treated are based on about 700 specimens, many of which had two to three identifiable species present. Plants of less than two to three square centimeters surface area and lacking reproductive structures or surface characteristics known to us from larger specimens were not treated. Almost 1000 units of species occurrence are employed in our ecological data.

The unit of occurrence is defined as the presence of an identifiable species on a specimen that is in almost all cases a block of "coralgal" substrate ranging from about 5–20 cm diam. The abundance figures cited in the following discussions refer simply to the number of samples within a given collection unit upon which a particular species occurs. Tabulation of the number of individual plants found within a collection would be less meaningful because of the tendency of adjacent plants of the same species to grow together and fuse without a trace of their former margins. Surface area occupied per species is a more desirable unit, but considering that the typical sample of coralline occupied substrate is a complex three-dimensional shape with several

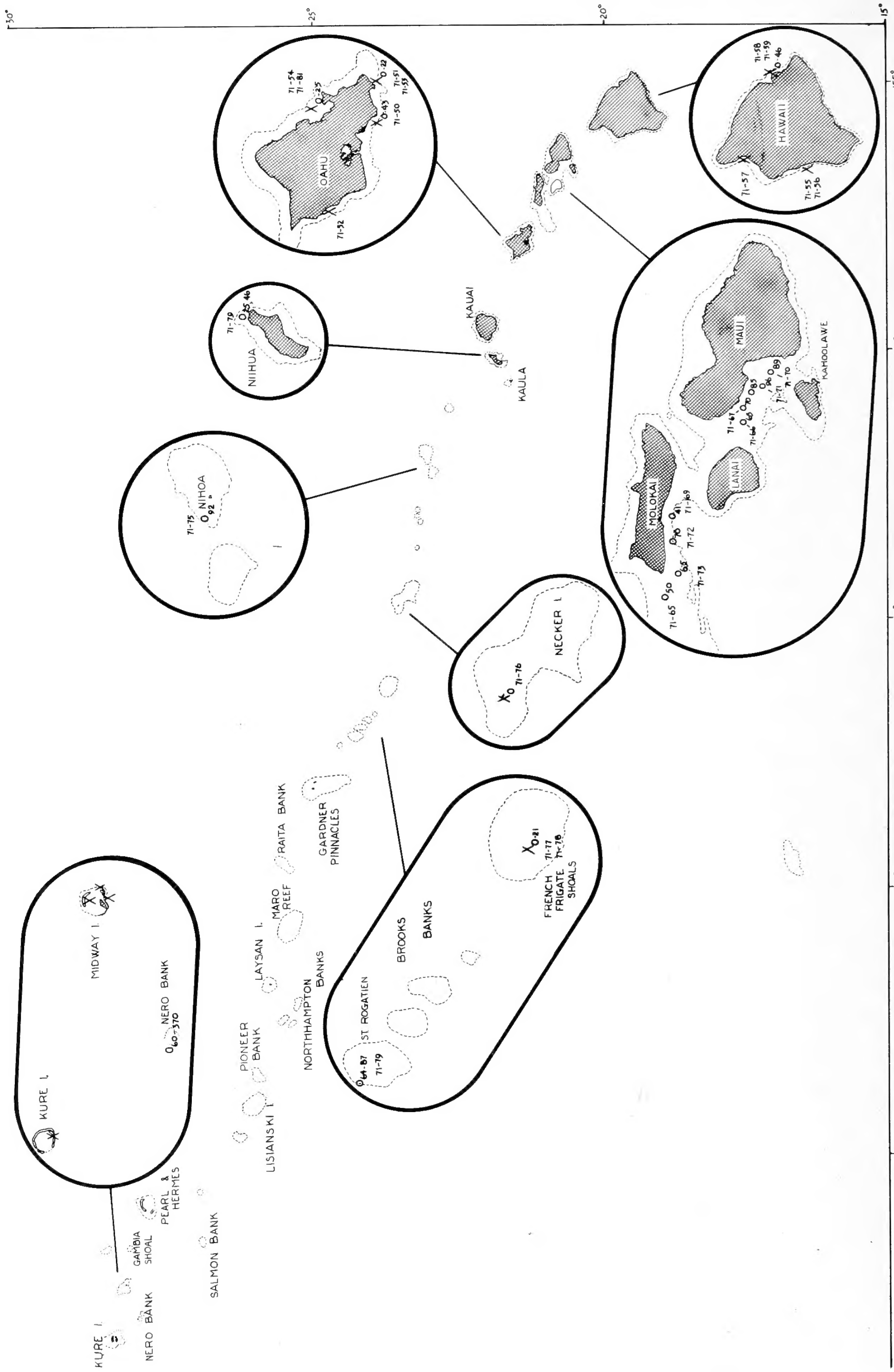


FIGURE 1.—Collection sites in the Hawaiian Islands.

spatial niches represented on each specimen, areal measurement would be time consuming and probably unnecessary in demonstrating the basic patterns of species distribution. The technique used by Littler (1971b) based on projecting surface coverage found within randomly selected areas is very effective on a relatively smooth surface lacking cryptic niches but is of limited usefulness on typical "coralgal" bottoms.

Ecological factors such as light, grazing, and epiphytes often alter the external appearance of coralline algae, and there can be considerable variation within a species. While we describe such morphological variation for certain taxa, other taxa are poorly known because of their limited number in the collections. A number of taxa for which we have inadequate data have been omitted from this paper. More intensive study in Hawaii and in more central parts of the Indo-Pacific will probably provide enough information on many of these less-abundant species to allow positive identification.

Taxonomy

One hundred seven species of crustose coralline algae previously described in many publications for the tropical-subtropical Indo-Pacific and tropical East Pacific were considered in this study. Fifty-four of these were described by Foslie from 1895 to 1929, isotypes of which are deposited in USNC. Nineteen species were described by Lemoine (1929), all but one from the tropical East Pacific; nine of these are represented by isotype fragments in our collection (USNC). Heydrich, from 1897 to 1901, described 12 of the species, though we have only two isotype fragments in our possession. Dawson, from 1944 to 1961, described 10 of the species considered, and although we have not been able to consult his type materials, his descriptions are extremely good and generally lead us to feel confident in their use. The Lemoine (1929) and Heydrich (1897a,b,c; 1901a,b,c) descriptions are often minimal, and where type material was not available, it was felt that we lacked an adequate understanding of the taxon in question. In these cases we followed the descriptions of Foslie.

All specimens, including the holotypes of the newly described species, are deposited in USNC.

Presentation of Material

In the taxonomic treatments, not all literature citations of previous species descriptions are given, but rather only those of particular significance or value in delineating the species in question. Only those taxa that are common have been treated fully. *Neogoniolithon frutescens* (Foslie) Setchell & Mason and *Mesophyllum siamense* (Foslie) Adey, although present, have not been included.

The following abbreviations are used in this study.

PC — Muséum d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris

TRH — herbarium of M. Foslie, Trondheim, Norway

UC — herbarium of the University of California

US — U.S. National Herbarium, Smithsonian Institution

USNC — Non-Articulate Coralline Algal Herbarium, National Museum of Natural History, Smithsonian Institution

CORALLINACEAE

Key to the Subfamilies and Genera

(Applies only to genera we encountered in Hawaii; see "Glossary" and Adey and Macintyre (1973) for discussion of terminology)

1. Tetrasporangia without caps, i.e., tetrasporangial conceptacles single pored 2

Tetrasporangia with caps, i.e., tetrasporangial conceptacles multipored (Melobesioideae) 7
2. Perithallial secondary pit connections present, cell fusions more or less rare or lacking (Lithophylloideae) 3
Perithallial secondary pit connections absent, cell fusions present (Mastophoroideae) 4
3. Perithallium palisade, single-layered hypothallium .... ***Tenarea***
Perithallium nonpalisade, single-layered or multilayered coaxial hypothallium .... ***Lithophyllum***
4. Heterocysts absent .... ***Lithoporella***
Heterocysts present 5
5. Hypothallium single layered .... ***Hydrolithon***
Hypothallium multilayered 6
6. Heterocysts vertical rows or single, hypothallium coaxial or simple-parallel to substrate .... ***Neogoniolithon***
Heterocysts loosely grouped into horizontal fields, hypothallium coaxial .... ***Paragoniolithon,*** new genus
Heterocysts grouped into tight horizontal pustulous fields, hypothallium simple-parallel or plumose .... ***Porolithon***
7. "*Lithothamnium*-type" cover cells not present, hypothallium coaxial .... ***Mesophyllum***
"*Lithothamnium*-type" cover cells present, hypothallium noncoaxial 8
8. Tetrasporangia in broad sori, partially calcified walls between adjacent sporangia .... ***Archaeolithothamnium***
Tetrasporangia in conceptacles, hypothallium simple-parallel .... ***Lithothamnium***

The first element in the key requires the presence of tetrasporic conceptacles. Although these are very often lacking in boreal-arctic plants (at least during the summer), they are frequently present in tropical corallines—if not on the surface, often buried in the thallus and visible upon fracture. If the nature of a single-pored conceptacle is uncertain, a quickly made slide (wet mount) will often indicate whether or not the contents are tetrasporangia. Even in the complete absence of diagnostic reproductive structures, very much can still be done on the generic level without paraffin sections. The following applies especially to the use of a high-powered dissecting microscope or reflecting compound microscope; hand sections, though time consuming, are equally useful.

The consistent presence of heterocytes and their grouping, along with the form of the hypothallium, delineates the four genera of Mastophoroideae: *Porolithon*, *Paragoniolithon*, *Neogoniolithon*, and *Hydrolithon*. Heterocysts do occur in *Mesophyllum*, although they tend to be small and scattered. A leafy plant with coaxial growth and few small heterocysts could be either a *Mesophyllum* or a *Neogoniolithon*. Reference to the species key and collection of more material for reproductive structures is required in this case.

In the Hawaiian saxicolous flora, the only *Tenarea* found is *T. tessellatum* (Lemoine) Littler, easily distinguished by its overlapping whorls (Figure 21). Similarly, no difficulty should be encountered in distinguishing the large-celled and leafy *Lithoporella melobesioides* (Foslie) Foslie (Figure 20).

Of the remaining species, the presence of secondary pit connections in abundance will place a plant in *Lithophyllum* or in the melobesioids. Some care is needed here, as *Archaeolithothamnium*

has abundant perithallial cell fusions, along with scattered secondary pit connections, or narrow or incipient fusions resembling secondary pit connections. *Lithophyllum* species also have a distinctive surface texture, which, although difficult to describe, is very helpful in initial separation of specimens: species with several epithallial cells are dull "chalky" in appearance; those with only a single epithallial cell are iridescent "chalky." *Porolithon* is the only genus with similar surface texture, but here the distinctive pustulous heterocyst fields are almost always present. *Archaeolithothamnium* plants can appear similar to the iridescent *Lithophyllum* plants, though the former are usually much darker red. A hand section is useful in this instance.

Among the remaining species, *Mesophyllum* plants are almost invariably leafy in habit and even if subsequently branched will often revert to the leafy habit between branches. The plants are characterized by a coaxial hypothallium, though careful orientation of a section parallel to the growth direction may be required to see this.

Archaeolithothamnium plants are characterized by a dark red-brown color and a quite glossy and smooth texture, whereas *Lithothamnium* and *Mesophyllum* are mostly pink to bluish-pink and dull in texture, often with surface micro-ridges. The "*Lithothamnium*-type" cover cells are quite distinctive for both *Lithothamnium* and *Archaeolithothamnium* but can be hard to determine with certainty without paraffin sections.

MASTOPHOROIDEAE (Svedelius) Setchell, 1943

Porolithon (Foslie) Foslie, 1909

Key to the Species

Plants crustose . . . . ***P. onkodes***
Plants branching . . . . ***P. gardineri***

Porolithon onkodes (Heydrich) Foslie

FIGURES 2–4

Porolithon onkodes (Heydrich) Foslie, 1909:57.—Gordon, Masaki, and Akioka, 1976.—Lee, 1967.—Lemoine, 1966.—Taylor, 1950.—Womersley and Bailey, 1970.
Lithothamnion onkodes Heydrich, 1897a:6, pl. 1: fig. 11.
Lithophyllum oncodes Heydrich, 1897c:410.
Goniolithon oncodes (Heydrich) Foslie, 1899:5.
Lithophyllum onkodes (Heydrich) Foslie, 1900a:8, 1903a; 1907a,b.—Weber-van Bosse and Foslie, 1904.
Porolithon oncodes (Heydrich) Foslie, 1909:57; 1929.—Littler, 1971b.
Lithophyllum (*Porolithon*) *oncodes* (Heydrich) Foslie, 1909:38.

DESCRIPTION.—Crusts well developed, lacking branches and excrescences, hemispherical in shape (Figure 2A), few mm to many cm thick, pink to yellow, with a rough appearance due to the abundance of heterocyst fields on the surface (Figure 2B,C). Epithallium a layer of rounded cells 1 to 3 cells thick (2–6 μm long, 5–9 μm diam.). Intercalary meristem large celled, occurring immediately below the epithallium (4–11 μm long, 4–8 μm diam.) (Figure 3). Perithallium multilayered, fusions common, cells 4–13 μm long and 4–10 μm diam. Heterocysts, 10–30 μm long and 4–14 μm diam., throughout perithallium forming compact fields to 100 μm diam. (Figure 2E,F). Hypothallium multilayered, plumose (Figure 2F), 50–150 (350) μm thick, may be thin with filaments oriented parallel to the substrate, cells 11–24 μm long and 5–14 μm diam. Tetrasporic conceptacles unipored, scattered, convex, small (240–300 μm outside diameter (O.D.), 110–230 μm inside diameter (I.D.), and 30–140 μm high), with roof apex about 40 μm above surface (Figure 2D), columella present; tetrasporangia 50–120 μm long and 20–50 μm diam., restricted to conceptacle periphery. Cystocarpic conceptacles unipored, slightly raised above surface, 150–210 μm I.D., 80–140 μm high; carpospores (35–70 μm long, 25–70 μm wide) arising from the periphery

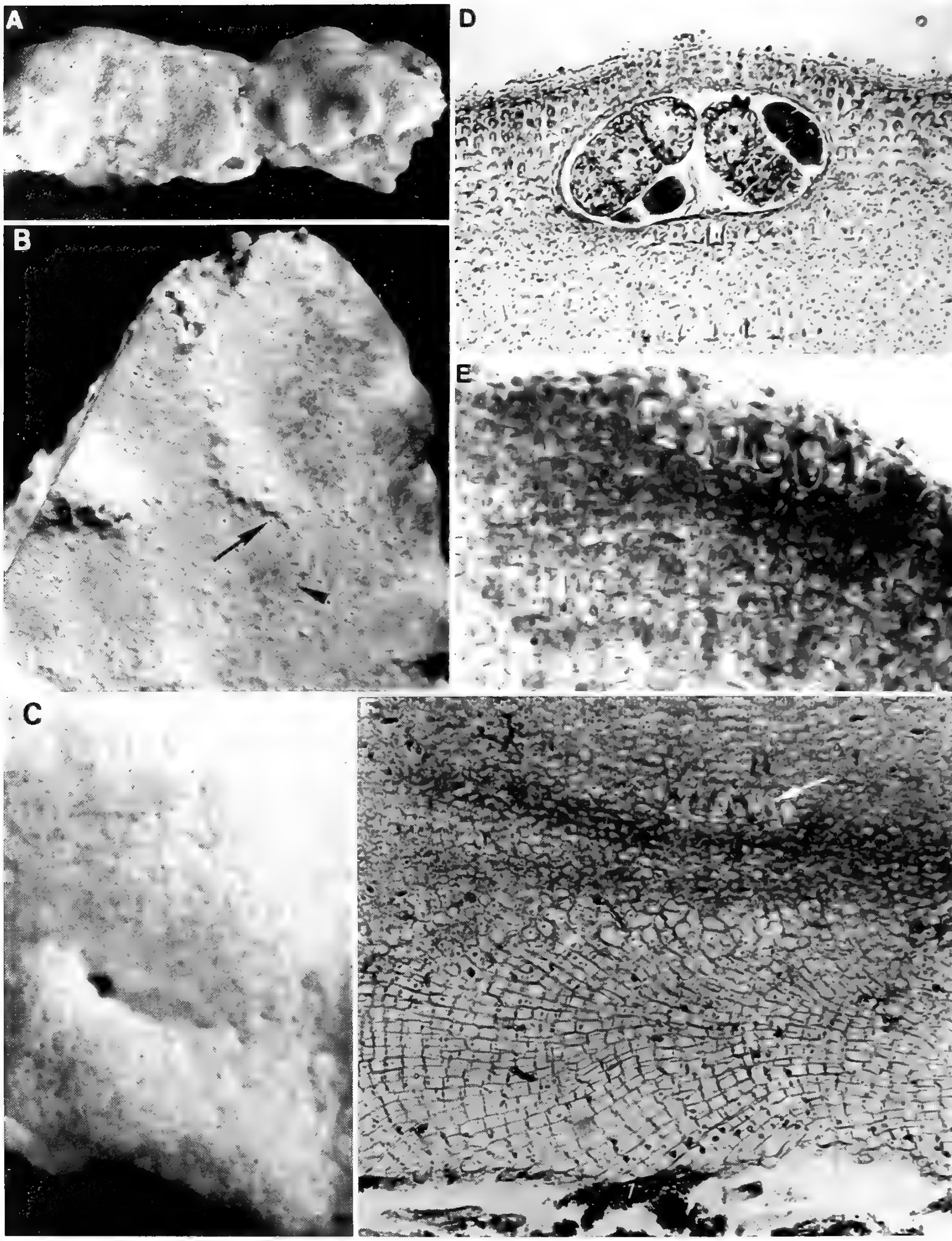


FIGURE 2.—*Porolithon onkodes:* A, habit, × 1; B, crust with tetrasporic conceptacle (arrow) and heterocyst fields (arrowhead), × 7; C, crust with heterocyst fields, × 12; D, tetrasporic conceptacle, × 250; E, heterocyst field at thallus surface, × 500; F, plumose hypothallium and buried heterocyst field (arrow), × 200. (Specimen nos.: A, B, 71-82-84; C, 71-82-85; D, 71-81-2; E, 71-82-76; F, 71-59-28; micrographs reduced to 85%.)

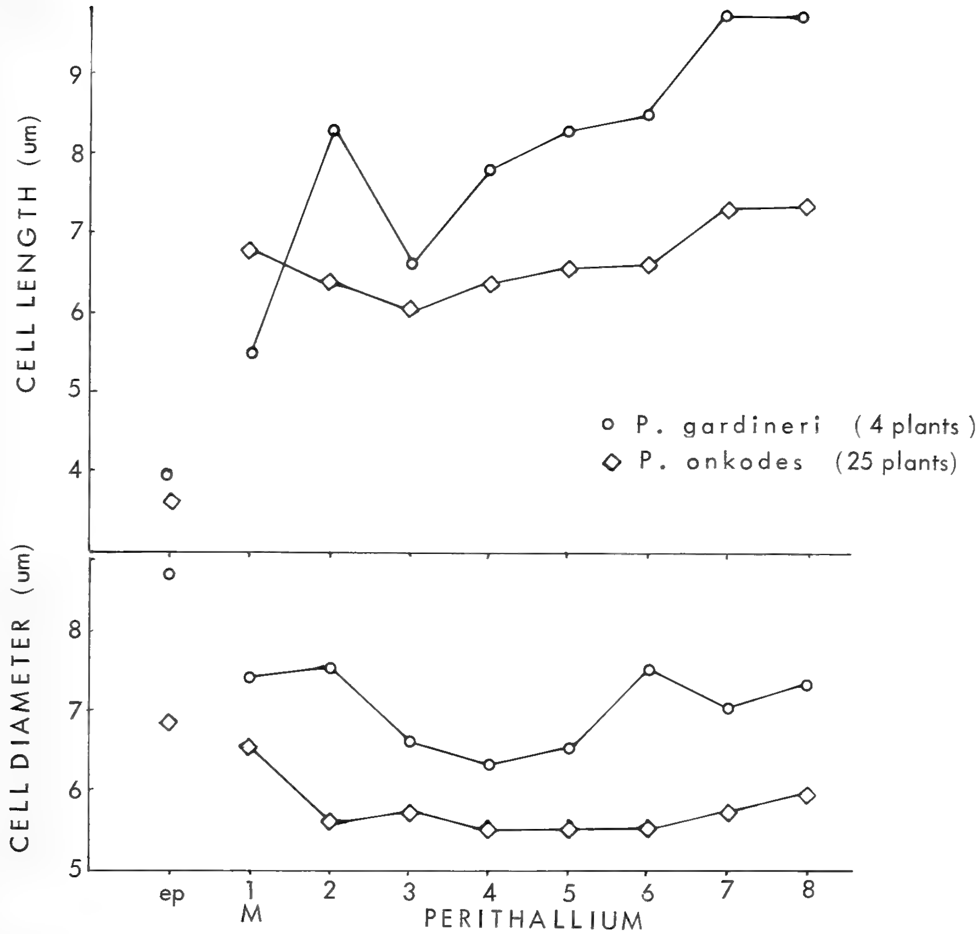


FIGURE 3.—Mean epithallial and perithallial cell dimensions in *Porolithon onkodes* and *P. gardineri*.

of a single discoid fusion cell. Male conceptacles unipored, slightly raised, 130–200 μm I.D., 20–35 μm high; spermatangial mother cells arising from the floor of the conceptacle only; spermatia at first elongate, crescent shaped, 3–5 μm long, 1–2 μm diam., becoming ellipsoidal.

TYPE-LOCALITY.—On coral ridges, Tami Island, northwest edge of the Huon Gulf, New Guinea.

HOLOTYPE.—Heydrich 97, March 1892, collected by Bambler, in herbarium of M. Foslie (TRH).

DISTRIBUTION.—Borneo, Easter Island, Funafuti Atoll, Guam, Hawaii, Marshall Islands, New Guinea, Solomon Islands, Sulu Archipelago, Indian Ocean, Maldives and Laccadives, Red Sea.

SPECIMENS STUDIED.—*Hawaii:* Hilo Bay, March 1971, 71-58-38, 71-59-28; Kawaihae, March 1971, 71-57-20. *Midway:* South Island, August 1971, 71-82-76, 71-82-84, 71-82-85. *Oahu:* Kaneohe Bay, March 1971, 71-54-4; August 1971, 71-81-2; Wainae, March 1971, 71-52-9.

REMARKS.—Only three sexual specimens were seen; all were monoecious. The male and female conceptacles are buried and occur at different levels in the thallus, indicating that *P. onkodes* inhibits self-fertilization by having different reproductive phases of the life cycle of any one plant maturing at different times. It was not clear whether there are two or four spermatia per spermatangial mother cell in *P. onkodes*. No pro-

carpic conceptacles were found in the Hawaiian specimens.

In shallow water, *P. onkodes* was the single most abundant species collected (Figure 4); over 50 percent of intertidal collections were *P. onkodes*. Individual plants of this species as small as one to two square centimeters are easily identified by the pustulous heterocyst fields over the thallus. Although *P. onkodes* is dominant in nearly all wave-beaten intertidal or uppermost sublittoral situations, it reaches its "peak of development" on algal ridges (Doty, 1974). Here it tends to dominate with the branched *Lithophyllum kotschyanum* Unger and the less abundant *Porolithon gardineri* (Foslie) Foslie occurring along the sides of channels and near low water. In the Caribbean, the very similar "pair species" (see "Glossary") *Porolithon pachydermum* (Foslie) Foslie and *Lithophyllum congestum* (Foslie) Foslie occur in the same ecological niches (Adey, 1979; Steneck and Adey, 1976). Borings through a number of high ridges in St. Croix, U.S. Virgin Islands, show that *Lithophyllum congestum* has been the dominant Holocene builder of these ridges (Adey, 1975). On the other hand, borings through the higher energy algal ridges of the easternmost Lesser Antilles have shown that *Porolithon pachydermum* and *Millepora* (Coelenterata) are the dominant builders of these more massive and higher algal ridges.

Porolithon gardineri (Foslie) Foslie

FIGURES 3–5

Porolithon gardineri (Foslie) Foslie, 1909:57.—Lee, 1967.—Littler, 1971b.—Taylor, 1950.

Lithophyllum gardineri Foslie, 1907a:190; 1929.

Lithophyllum (Porolithon) gardineri Foslie, 1907b:30; 1909.

DESCRIPTION.—Crusts weakly developed, quickly producing branches initially simple, terete, 1.5–3 mm diam., slightly tapering and with rounded tops (Figure 5A); branches typically becoming complexly branched, often flattened, fused and anastomosing to produce 12 cm or larger hemispheric heads (quiet-water forms with delicate branches, 1–2 mm diam., are known and discussed below); pink to yellow, with a granular texture as in *P. onkodes*; the heterocyst fields crowded and more pustulous than *P. onkodes* with a marked upturned epithallial rim. Epithallium a single layer of cells, 3–5 μm long, 8–10 μm diam. Perithallium multilayered, fusions common, cells 5–10 μm long and 6–11 μm diam (Figure 3). Heterocysts throughout perithallium, 13–26 μm long and 7–15 μm diam. Hypothallium not measured. No conceptacles, asexual or sexual, were seen in sections of our material.

TYPE-LOCALITY.—Coetivy, Seychelle Islands, Indian Ocean.

LECTOTYPE.—Gardiner sn., September 1905, in herbarium of M. Foslie (TRH) (Adey, 1970). Lecto-isotype: USNC.

DISTRIBUTION.—Hawaii, Indian Ocean, Marshall Islands.

SPECIMENS STUDIED.—*Oahu:* Kanehoe Bay, March 1971, 71-54-5. *Midway:* March 1971, 71-60-3; August 1971, 71-82-37.

REMARKS.—As in *P. onkodes*, normal plants of

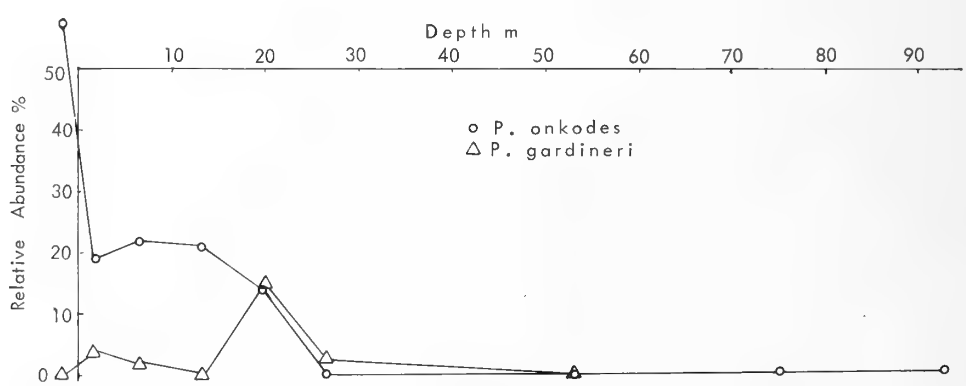


FIGURE 4.—Depth distribution of *Porolithon onkodes* (o) and *P. gardineri* (△) in Hawaii.

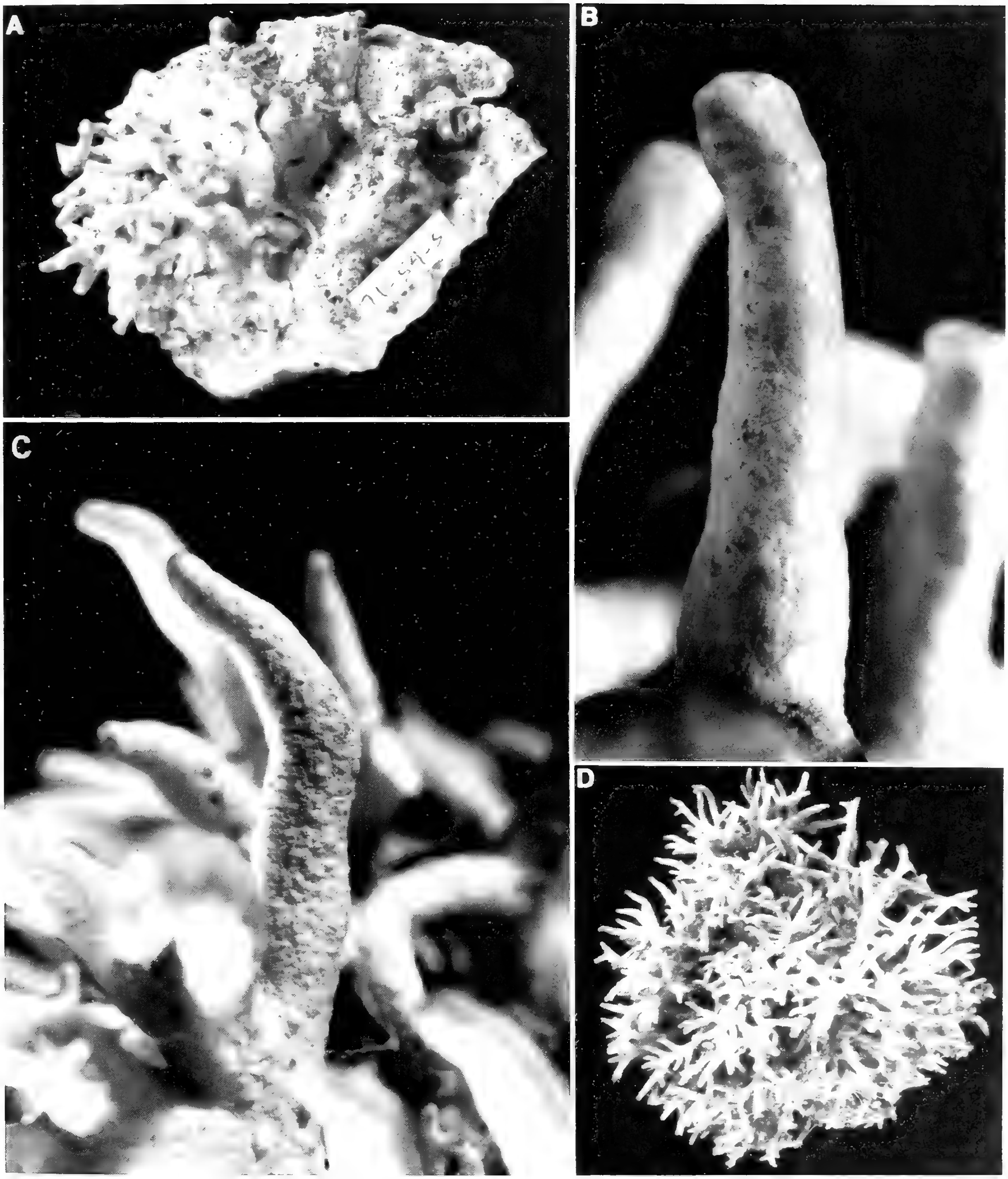


FIGURE 5.—*Porolithon gardineri:* A, habit of typical specimen, × 1; B, branch showing smooth surface from limpet grazing, × 10; C, branch showing characteristic heterocyst fields, × 10; D, habit of specimen from Midway Island lagoon, × 1. (Specimen nos.: A, B, 71-54-5(a); C, D, 71-60-3; micrographs reduced to 96%.)

P. gardineri have markedly distinct, pustulous heterocyst fields (Figure 5C); however, micrograzing, probably by young limpets and perhaps chitons, can remove this pustulous surface (Figure 5B). Because of grazing effects on morphology, care must be taken not to misidentify this species with externally similar *Lithophyllum kotschyanum*. The chalky pink-yellow surface of *P. gardineri*, as opposed to the red-brown, glossy surface of *L. kotschyanum*, is usually a distinctive characteristic even in the absence of heterocyst fields.

Steneck and Adey (1976) have shown with transplants that the marked variety of branch form in the Caribbean *Lithophyllum congestum* is a function of microenvironment. This plant had been separated into several species by Foslie (Steneck and Adey, 1976). A wide variety of branch form is also to be seen in the Hawaiian *Porolithon gardineri* and *Lithophyllum kotschyanum* (see below). At a single station in the lagoon of Midway Atoll, a fine-branched *Porolithon* (Figure 5D) that is tentatively placed in *P. gardineri* was found in abundance (it was not included in the measurements). Its surface texture is very similar to that of the *P. gardineri* found in the remainder of our stations, and the branching patterns are similar, though markedly smaller than *P. gardineri*, having diameters of 1–2 mm.

As discussed above, *P. gardineri* is primarily a shallow sublittoral plant. In contrast to the situation on central Pacific atolls (Lee, 1967), on Hawaiian algal ridges it is exceeded in abundance by the branching *L. kotschyanum*. The "peak" of abundance of *P. gardineri* appears at a depth of 18 m (Figure 4) and results largely from its occurrence at that depth at a single station, on the south side of East Island, Midway Atoll. The small, secondary peak at 0 to 3 m is more characteristic for the species in the algal ridge environment.

***Paragoniolithon*, new genus**

DESCRIPTION.—Thallus crustosum ad faliaceum, non ramosus. Epithallium ex unico strato cellularum rotundatarum constans, membranis exterioribus tangentialibus incrassatis. Perithallium pluristratosum, fusionibus frequentibus. Heterocystae in stratis horizontalibus plerumque laxe aggregatae e duabus tribusve cellulis, cellula exteriore protuberatione praedita compositae. Hypothallium pluristratosum, crassum, leniter ad valde coaxiale. Conceptacula tetrasporangialia uniporata; tetrasporangia adsunt, bisporangia rara, ad periferiam conceptaculi restricta. Conceptacula spermatialia uniporata; cellulae-matricales spermatangiales duas ad quattuor excrescentias spermatiales habentes, ad pavimentum conceptaculi restrictae; spermatia ellipsoidae. Plantae carpogoniales cystocarpicaeque rarae.

Thallus crustose to leafy, unbranched. Epithallium a single layer of rounded cells; outer tangential wall thickened. Perithallium multilayered, fusions common. Heterocysts generally loosely grouped into horizontal fields composed of 2–3 cells, outer cell with protuberance. Hypothallium multilayered, thick, weakly to strongly coaxial. Tetrasporangial conceptacles uniporate; tetrasporangia present, bisporangia rare, restricted to the periphery of the conceptacle. Spermatial conceptacles uniporate; spermatangial mother cells with 2–4 spermatial outgrowths; restricted to the floor of the conceptacle; spermatia ellipsoidal. Carpogonial and cystocarpic plants rare.

TYPE-SPECIES.—*Paragoniolithon solubile* (Foslie & Howe in Foslie), new combination.

Basionym: *Goniolithon solubile* Foslie & Howe in Foslie, 1907c:21; Boyd, Kornicker, and Rezak, 1963; Howe, 1920; Taylor, 1928, 1960. Recombinations as follows:

Neogoniolithon solubile (Foslie & Howe in Foslie) Setchell & Mason, 1943:90.—Adey, 1970.
Goniolithon propinquum Foslie, 1929:31.
Neogoniolithon propinquum (Foslie) Lemoine, 1966:14.—Papenfuss, 1968.

TYPE-LOCALITY.—Culebra Island, Puerto Rico.

LECTOTYPE.—Howe, 4375, in herbarium of M. Foslie (TRH) (Adey, 1970). Lecto-isotype: USNC.

DISTRIBUTION.—Tropical seas, typically at moderate depths, 5–25 m, in reef environments.

Paragoniolithon conicum (Dawson), new combination

Figures 6, 7

Hydrolithon conicum Dawson, 1960a:27. [Basionym.]
Neogoniolithon conicum (Dawson) Gordon, Masaki, & Akioka, 1976:259.—Zhang and Zhou, 1980.

Description.—Crusts firmly adherent, 0.5 to several mm thick, unbranched (Figure 6A), often draped over the basal parts of finger corals; frequently deep red but ranging from yellow-pink to maroon, margin smooth to undulating, within several mm to 1 cm from the margin very abundant nonpustulous heterocyst fields develop (50–100 μm diam) (Figure 6A,B) giving the surface a slightly rough appearance. Epithallium a single layer of rounded cells, 3–9 μm diam. Intercalary meristem cells elongate, cells 4–9 μm long and 5–10 μm diam., with some progressive elongation occurring throughout the perithallium (Figure 7).

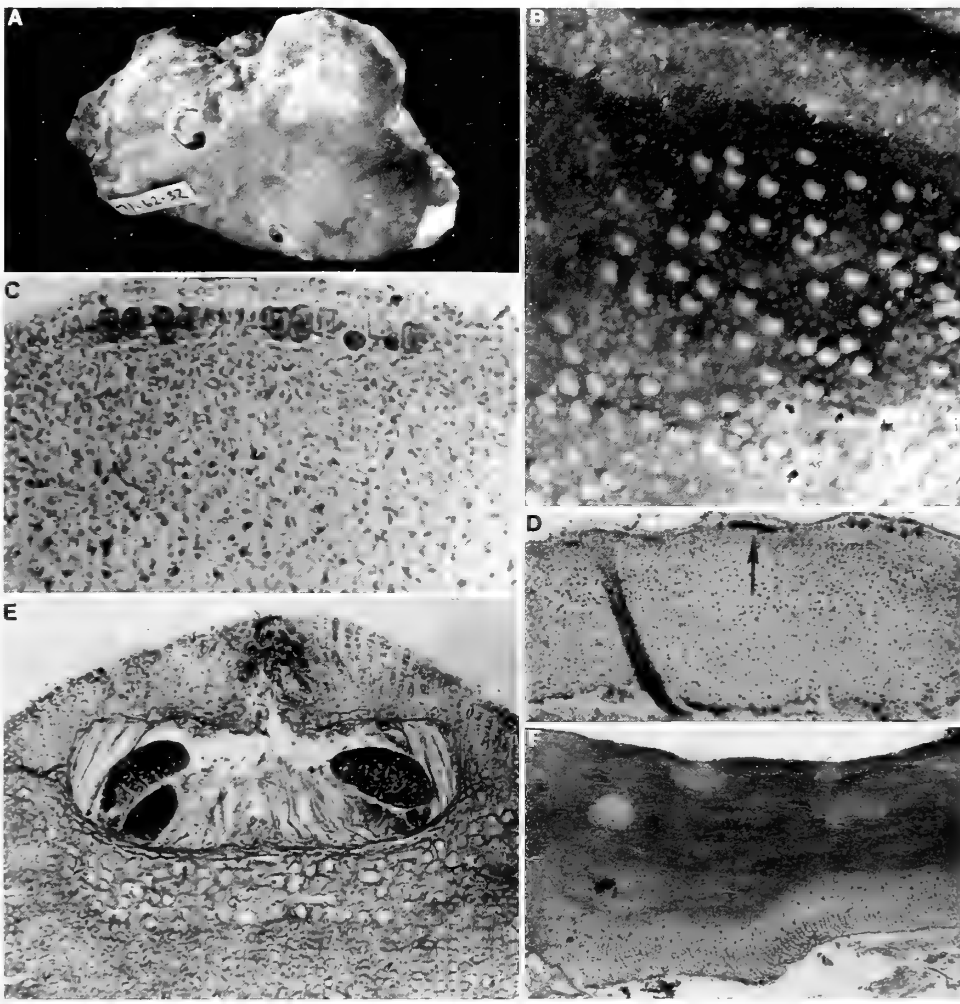


Figure 6.—*Paragoniolithon conicum:* A, habit of typical specimen, × 1; B, surface features including tetrasporangial conceptacles, × 10; C, section through thallus showing heterocyst field, × 200; D, section through vegetative thallus in region of heterocyst fields (arrow), × 40; E, section through tetrasporangial conceptacle, × 250; F, section through vegetative thallus showing coaxial hypothallium, × 35. (Specimen nos.: A, B, E, 71-62-32; C, D, 71-78-13; F, 71-55-35; micrographs reduced to 70%.)

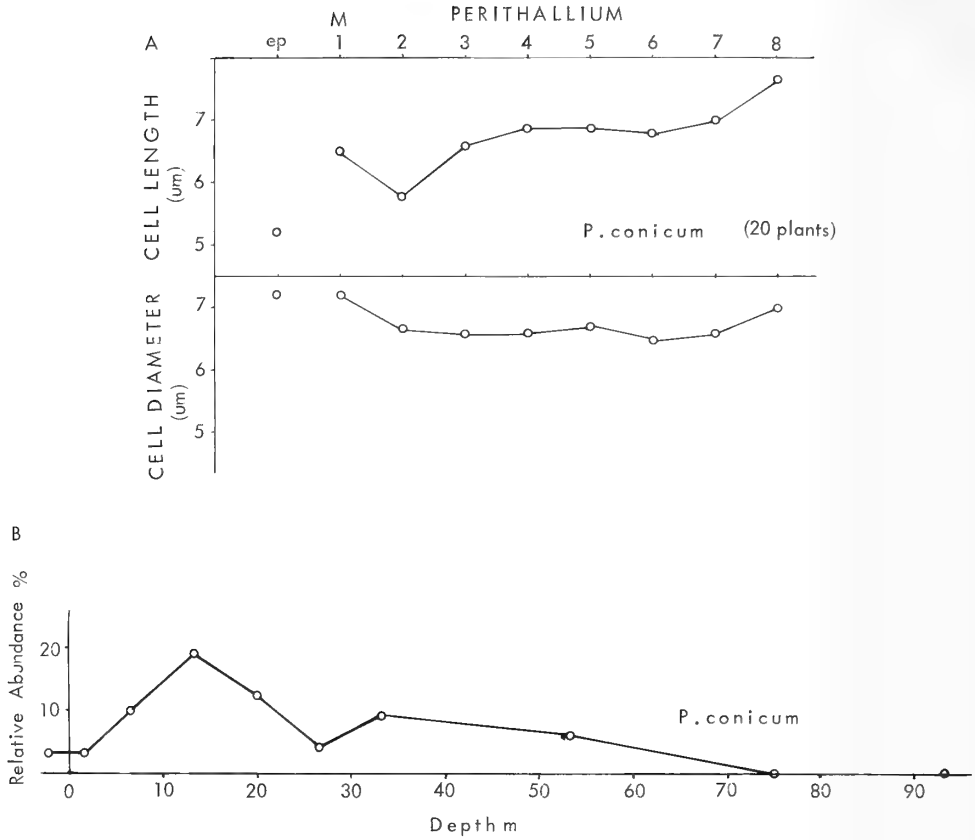


FIGURE 7.—*Paragoniolithon conicum:* A, mean epithallial and perithallial cell diameter and length; B, depth distribution.

Perithallium multilayered, fusions abundant, cells 3–11 μm long and 4–13 μm diam. (Figures 6C, 7). Heterocyst fields throughout the perithallium, loose, with scattered filaments between the heterocysts (Figure 6C,D), heterocysts 7–26 μm long and 8–21 μm diam. Hypothallium parallel to substrate, weakly to strongly coaxial, 30–400 μm thick; cells 8–25 long and 4–16 μm diam. (Figure 6F). Tetrasporic conceptacles unipored, regularly spaced, convex, conical, small (350–530 μm O.D., 140–360 μm I.D., 50–160 μm high), strongly raised, roof apex 40–200 μm above plant surface (Figure 6E), columella present; tetrasporangia restricted to the periphery of the conceptacle, 80–200 μm long, 45–65 μm diam. No procarpic or cystocarpic material found in our specimens. Male conceptacle unipored, 190–260 μm I.D., 40–80 μm high, raised but more rounded than tetrasporangial conceptacle; spermatangial mother cells arising from the base of the conceptacle only; spermatia ellipsoidal, 3–6 μm long, 1–3 μm diam.

TYPE-LOCALITY.—Intertidal reef at Binners Cove, Isla Socorro, Revillagigedo Archipelago, Pacific Mexico.

HOLOTYPE.—Dawson, 12148, 19 November 1953, (US).

DISTRIBUTION.—Xisha Islands, China; Guam; Pacific Mexico.

SPECIMENS STUDIED.—*French Frigate:* La Perouse, August 1971, 71–78–13. *Hawaii:* Honaunau Bay, March 1971, 71-55-34, 71-55-35. *Midway:* Lagoon, March 1971, 71-62-32. *Oahu:* Honauma Bay, March 1971, 71-53-7; Waikiki, March 1971, 71-50-45.

REMARKS.—The type collection (Dawson,

1960a) includes only bisporic specimens. Bisporic plants were not found in our collections; we did, however, have tetrasporic plants. The description of *P. conicum* should therefore be emended to include tetrasporic plants. Formation of the tetrasporic conceptacles follows the "sur-type" of Johansen (1976) with the presence of a central columella (see Townsend, 1981).

Only one sexually reproductive specimen, a male, was collected. Formation of the male conceptacle is similar to that described for *Lithothamnium* by Lebednik (1978). The first indication of formation of the male conceptacle is cessation of an area of intercalary meristem cells. These cells become the prospective spermatangial mother cells (PSMC). The epithallium separates from the PSMC layer, which changes from a columnar to conical shape. The surrounding vegetative filaments continue dividing and grow in over the fertile area forming the conceptacle roof. As the roof forms, the apex of the PSMC elongates and "cuts off" a spermatium into the conceptacle cavity. It is not clear how many times this may occur per mother cell. Spermatangial production is restricted to the conceptacle floor. The spermatia are at first ellipsoidal, then discoid, and may congregate in long mucus streams in the conceptacle cavity. The single pore of the conceptacle remains plugged during spermatial production with a substance not stained with phosphotungstic hemotoxylin.

This species is illustrated on the "Finger Coral: Hawaii" coral reef commemorative stamp issued by the U.S. Postal Service, 26 August 1980.

Paragoniolithon conicum occurs commonly in mid-depths (Figure 7) at all stations from Midway to Hawaii. From 9 to 15 m, *P. conicum* and *P. onkodes* were the most frequent crustose coralline algae (19% of the specimens collected). Although *P. conicum* occurs on a variety of "coralgal" sub-substrate, it appears to especially prefer the sides of finger corals, and by gradually growing up from below, may eventually kill living coral.

Two species of *Paragoniolithon*, *P. solubile* and *P. "typica"* (nomen nudum: Adey, 1979) occur in the Caribbean and occupy similar substrate and depth ranges (Adey, 1979); however, unlike many of the "pair species" discussed here, *P. conicum* seems to be rather distinct from its Caribbean counterparts. This would indicate that *Paragoniolithon* has evolved more rapidly than most tropical coralline algae and that their habitat, "sides of finger corals," is relatively new for coralline algae.

Neogoniolithon Setchell & Mason, 1943

Key to the Species

1. Plants thin crusts, rugulose; low-domed conceptacles < 200 μm O.D. .... ***N. rugulosum,*** new species
   Plants thicker, not rugulose, conceptacle > 200 μm O.D. 2
2. Crusts adherent, knobby, bright pink to yellow brown, conceptacles 200–400 μm O.D. .... ***N. rufum,*** new species
   Crusts leafy to sub-leafy, pink yellow to dark brown, conceptacles > 400 μm O.D. 3
3. Crusts sub-leafy, but eventually developing abundant rounded, often club-shaped irregular protuberances, conceptacles high conical, leaving scars on surface after spores dispersed .... ***N. clavacymosum,*** new species
   Crusts sub-leafy, becoming thick (to 5 mm) without protuberances, conceptacles low conical, leaving no scars .... ***N. fosliei***

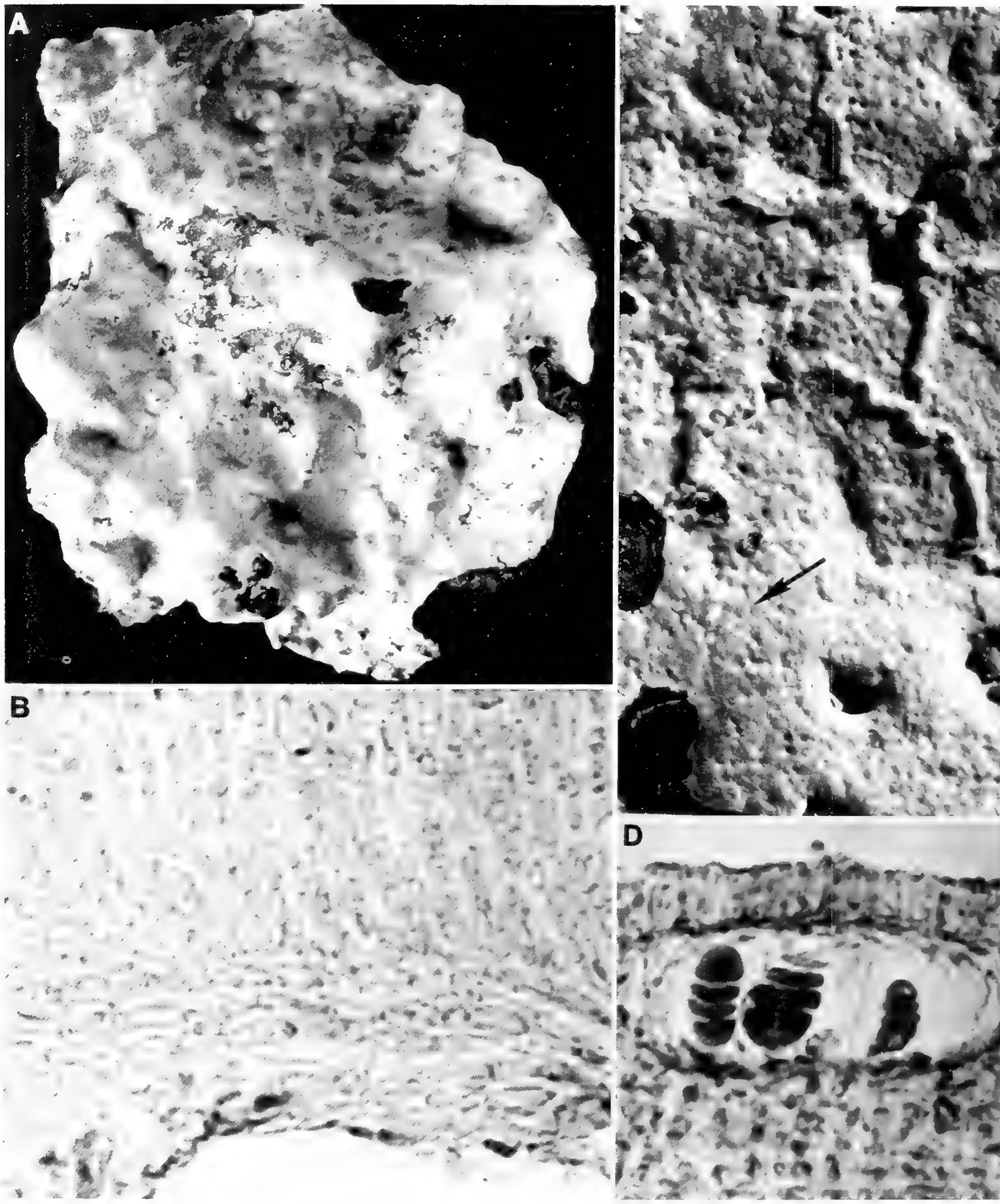


FIGURE 8.—*Neogoniolithon rugulosum*, new species: A, habit of type specimen, × 1; B, hypothallium of type specimen, × 500; C, surface showing rugulose nature of crust, note conceptacles (arrowed), × 10; D, tetrasporangial conceptacle, × 600. (Specimen nos.: A, B, 71-53-2; C, 71-59-1; D, 71-53-4.)

Neogoniolithon rugulosum, new species

FIGURE 8

DESCRIPTION.—Crustae tenues (< 200 μm), rugulosae, maculas subtiles albas saepe praebentes; multa conceptacula parva tholiformia, aut eorum cavos (Figura 8A,C) haventes, colore rosacea ad flavo-rosaceam. Epithallium ex uno duobusve stratis cellularum tholiformium constans, membrana in membranis exterioribus tangentialibus radialibusque spissescens; cellulae 5–12 μm long. atque 9–16 μm diam. Meristema intercalare elongatum, admodum infra epithallium, cellulis 10–19 μm long. atque 6–10 μm diam. Perithallium multis cellulis crassum (Figura 8B), fusionibus frequentibus, cellulis 4–8 μm long atque 3–6 μm diam. Heterocystae per perithallium dispersae, singulae, raro in coacervationibus horizontalibus repertae, 12–14 μm long atque 7–9 μm diam. Hypothallim e 2–8 stratis celularum constans (Figura 8B), subparallelum ad substratum, 25–75 μm crass.; cellulae 9–30 μm long atque 6–15 μm diam. Conceptacula tetrasporica uniporata (160–200 μm O.D., 70–90 μm I.D., 30–50 μm alt.) tecta plana ad paululum tholiformia super crustas circumdantes; tetrasporangia trans pavimentum conceptaculi disposita, 50–85 μm long atque 25–50 μm diam (Figura 8D).

Crusts thin (< 200 μm), rugulose, often with fine white speckles; abundant small domed conceptacles or their cavities (Figure 8A,C); pink to yellow pink. Epithallium 1 to 2 layers of domed cells, wall thickening on outer tangential and radial walls; cells 5–12 μm long and 9–16 μm diam. Intercalary meristem elongate, immediately below epithallium, cells 10–19 μm long and 6–10 μm diam. Perithallium, many cells thick (Figure 8B), fusions common, cells 4–8 μm long and 3–6 μm diam. Heterocysts scattered throughout perithallium, single rarely in horizontal assemblages, 12–14 μm long and 7–9 μm diam. Hypothallium 2–8 cell layers (Figure 8B), subparallel to substrate, 25–75 μm thick; cells 9–30 μm and 6–15 μm diam. Tetrasporic conceptacles single pored, 160–200 μm O.D., 70–90 μm I.D., 30–50 μm high, roofs flat to slightly domed above surrounding crusts; tetrasporangia across floor of conceptacle, 50–85 μm long and 25–50 μm diam. (Figure 8D). No sexual material collected in present study.

TYPE-LOCALITY.—Palea Point, Hanauma Bay, Oahu, Hawaii (21°07′N,157°50′W), on volcanic rock, intertidal zone.

HOLOTYPE.—D. Child, 71-53-2, 1 April 1971 (USNC), Figure 8A,B

PARATYPES.—*Hawaii:* Hilo Bay, March 1971, 71-59-1. *Oahu:* Honauma Bay, March 1971, 71-53-22, 71-53-4.

DISTRIBUTION.—Hawaii and Oahu, Hawaii.

REMARKS.—The specific epithet *rugulosum* describes the surface, a feature distinguishing our new taxon from other Hawaiian members of the genus.

We have only a few specimens of this species from bedrock and from volcanic and terrigenous pebbles in the intertidal and uppermost sublittoral. Its sparseness in our collections may, however, only indicate considerable difficulty in collecting it from wave-beaten rocks rather than its rarity. A "pair species," *Neogoniolithon caribaeum* (Foslie) Adey, is known from the Caribbean (Adey, 1979).

Neogoniolithon rufum, new species

FIGURES 9–11A

DESCRIPTION.—Crustae primum satis tenues, marginibus arcte adhaerentibus (Figura 9A), 1–2 mm crass. factae, superficies saepe clare rosacea ad fusco-brunneam, autem, varians, levis, opalescens (Figura 9B), conceptacula super thallum catervatim aggregata. Epithallium ex uno strato cellularum rotundatarum constans, incrassationes membranae esterioris tangentialis perspicuae; cellulis 2–6 μm long. atque 4–9 μm diam. Meristema intercalare parum elongatum, cellulis 3–9 μm long. atque 3–10 μm diam. Perithallium pluristratosum, aliquantula elongatione effecta (Figura 10), fusionibus frequentibus, abrupte zonatum (Figura 9A), cellulis 3–11 μm long. atque 2–11 μm diam. Heterocystae singulae, interdum

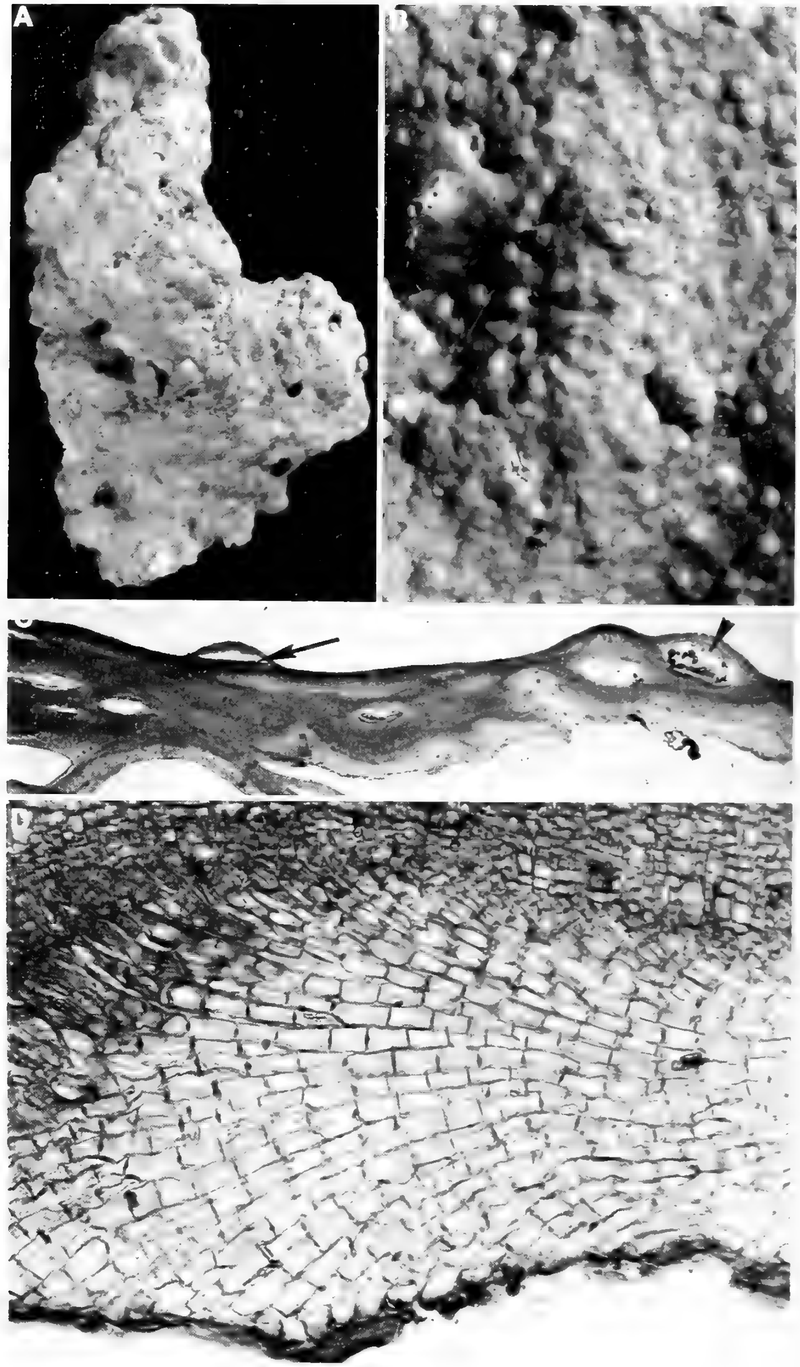


FIGURE 9.—*Neogoniolithon rufum*, new species: A, habit of type specimen, × 1; B, thallus surface, note strongly raised tetrasporic conceptacles, × 10; C, section through monoecious crust, note male conceptacle (arrow) and cystocarpic conceptacle (arrowhead), × 40; D, hypothallium, × 350. (Specimen nos.: A, B, 71-50-80; C, 71-82-57; D, 71-50-20; micrographs reduced to 89%.)

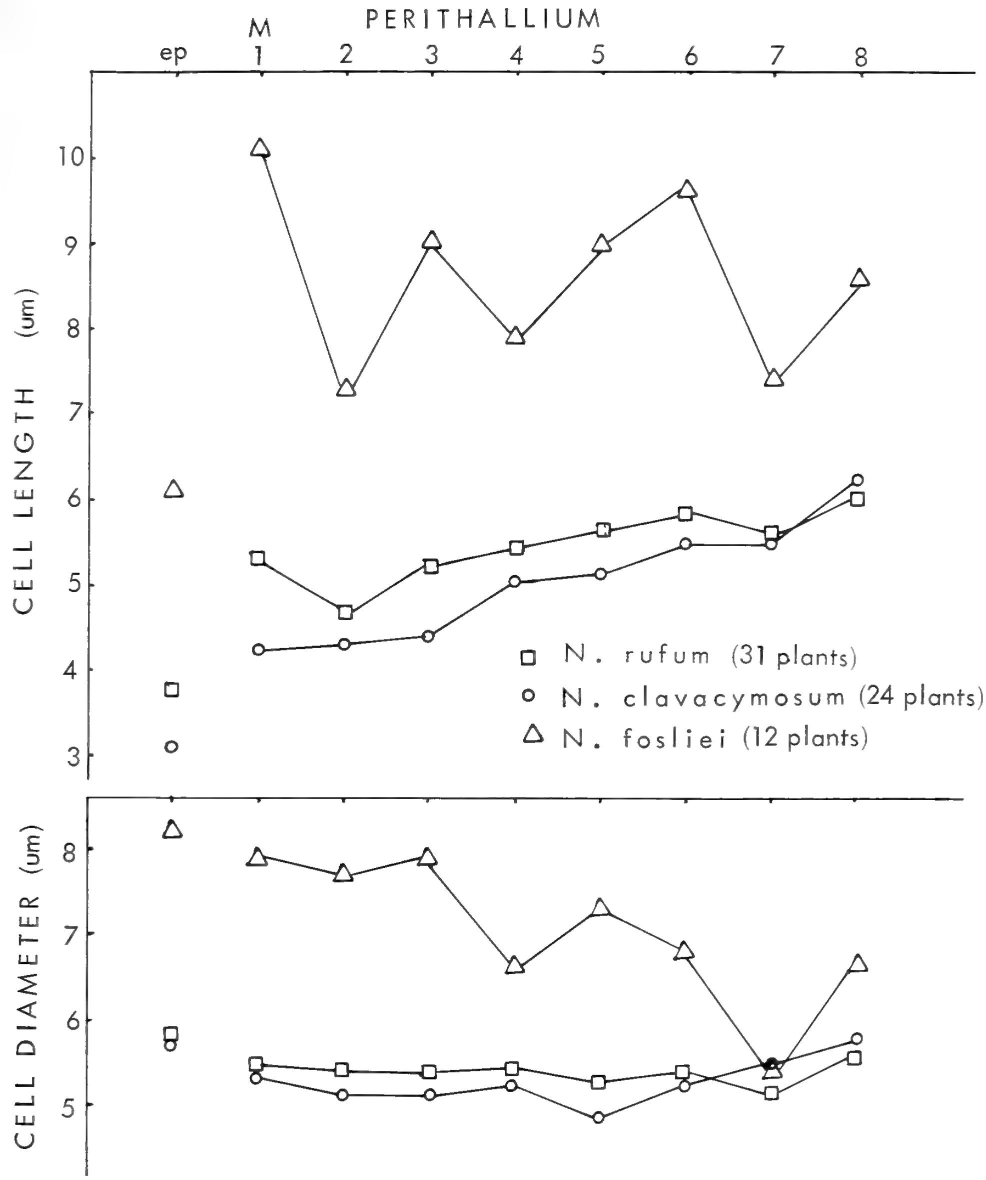


FIGURE 10.—Cell diameter and length data for *Neogoniolithon rufum*, new species, *N. clavacymosum*, new species, and *N. fosliei*.

rarae (aliqunado laxe verticaliter horizontaliterque aggregata) 7–29 μm long. atque 4–12 μm diam. Hypothallium simplex ad coaxiale, ad substratum parallelum (Figura 9D), 25–130 (200) μm crass., cellulis 9–25 μm long. atque 4–10 μm diam. Conceptacula tetrasporica uniporata, 30–150 μm super crustam elevata (Figura 9B), 200–400 μm O.D., 80–300 μm I.D. atque 50–110 μm alt., per perithallium obruta; tetrasporangia 50–175 μm long. atque 29–65 μm diam. super totum pavimentum conceptaculi disposita. Conceptaculum procarpicum uniporatum, 380 μm I.D., atque 100 μm alt., omnis cellula sustinens duo initia carpogonialia ramorum habens. conceptacula cystocarpica uniporata, 210–290 μm I.D. atque 60–90 μm alt., per perithallium cum sporis obruta; carposporae 50–70 μm long. atque 40–70 μm diam., solum in periferia cellulaecoalescentis magnae

discoideae dispositae (285–340 μm diam.) (Figura 9C). Conceptaculum masculum uniporatum, 50–130 μm elevatum, 215–350 μm I.D. atque 50–100 μm alt.; spermatia ad pavimentum conceptaculi restricta (Figura 9C); 2–4 spermatia in omni cellulamatricalee, ellipsoidea ad discoidea (3–7 μm long., 2–3 μm diam.).

Crusts initially quite thin with closely adherent margins (Figure 9A), becoming 1–2 mm thick, surface often bright pink though ranging to dark brown, smooth, opalescent (Figure 9B), conceptacles distributed in groups over the thallus. Epithallium a single layer of rounded cells, outer tangential wall thickenings marked; cells 2–6 μm long and 4–9 μm diam. Intercalary meristem weakly elongate, cells 3–9 μm long and 3–10 μm diam. Perithallium multilayered, some elongation occurring (Figure 10), fusions common, sharply zonate (Figure 9C), cells 3–11 μm long and 2–11 μm diam. Heterocysts single, sometimes rare (occasionally grouped loosely vertically and horizontally) 7–29 μm long and 4–12 μm diam. Hypothallium simple to coaxial, parallel to substrate (Figure 9), 25–130 (200) μm thick, cells 9–25 μm long and 4–10 μm diam. Tetrasporic conceptacles unipored, raised 30–150 μm above the crust (Figure 9B), 2001–400 μm O.D., 80–300 μm I.D., and 50–110 μm high, buried throughout perithallium; tetrasporangia 50–175 μm long and 29–65 μm diam., over entire conceptacle floor. Procarpic conceptacle unipored, 380 μm I.D. and 100 μm high, 2 carpogonial branch initials per supporting cell. Cystocarpic conceptacles unipored, 210–290 μm I.D. and 60–90 μm high, buried throughout perithallium with spores; carpospores 50–70 μm long and 40–70 μm diam., only on the periphery of the large discoid fusion cell (285–340 μm diam.) (Figure 9C). Male conceptacles unipored, raised 50–130 μm above surface, 215–350 μm I.D. and 50–100 μm high; spermatia restricted to conceptacle floor (Figure 9C), 2–4 spermatia per mother cell, ellipsoidal to discoid 3–7 μm long, 2–3 μm diam.

TYPE-LOCALITY.—Waikiki, Oahu, Hawaii (21°15′N, 157°35′W), on coral rubble, 130 m.

HOLOTYPE.—D. Child, 71-50-80, 27 March 1971 (USNC), Figure 9A.

PARATYPES.—*French Frigate:* La Perouse, August 1971, 71-78-14. *Hawaii:* Hilo Bay, March 1971, 71-58-14. *Oahu:* Kaneohe Bay, August 1971, 71-81-28; Waikiki, March 1971, 71-50-20, 71-50-31, 71-50-72, 71-50-80. *Midway:* South Island, August 1971, 71-82-57.

DISTRIBUTION.—Throughout Hawaiian Archipelago.

REMARKS.—The specific epithet refers to the unique color of *N. rufum*.

The formation of the male conceptacles is similar to that for *Paragoniolithon conicum*. In *Neogoniolithon rufum* there are two to four spermatangial projections from each mother cell. As in *P. conicum*, spermatia aggregate into chains within the conceptacle cavity. Carpospores are restricted to the periphery of the cystocarpic conceptacle. This contrasts to the pattern seen in *Neogoniolithon accretum* (Foslie & Howe) Setchell & Mason and *Neogoniolithon pacificum* (Foslie) Setchell & Mason (Masaki, 1968).

Monoecious thalli with cystocarpic and spermatangial conceptacles were seen (Figure 9C). Both conceptacle types were buried with contents in the thallus but do not show layering as in *Porolithon onkodes*. One hermaphroditic conceptacle was seen. This phenomena in crustose corallines has only been recorded for *Phymatolithon lenormandii* (Areschoug) Adey (Adey, 1966) and *Synarthrophyton patena* (J.D. Hooker & Harvey) Townsend (Townsend, 1979). In *Neogoniolithon rufum* half the conceptacle was male, and the other half procarpic. Only one procarpic conceptacle was seen. Two carpogonial branch initials arise from the support cell. One or both of these may extend and undergo division to form a carpogonium and hypogynous cell. Therefore, *N. rufum* has procarps with two carpogonial branches or one carpogonial branch and one sterile cell per supporting cell. This pattern differs from that of *Neogoniolithon accretum* and *N. pacificum* (Masaki, 1968) with only one carpogonial branch per procarp.

Neogoniolithon rufum, *Paragoniolithon conicum*, and

Tenarea tessellatum together dominate the shallow to mid-depth coralline flora, although *P. onkodes* is abundant in water less than 20 m. The former three species occur on 25% of the collected specimens from low water to depths of nearly 50 m. *Neogoniolithon rufum* tends to be a little more abundant at the lower part of this range than the other species (Figure 11A). Also, while the sympatric *Paragoniolithon conicum* and *Tenarea tessellatum* have Caribbean "pair species," *N. rufum* does not.

Neogoniolithon clavacymosum, new species

FIGURES 10, 11B, 12

DESCRIPTION.—Crustae bene evolutae amplae factae, ramos breves simplicesque sparsos, qui irregulariter clavati atque saepe nodulosi fiunt (Figura 12A,B) efficientes; margines leves crassique, foliosi et ad substratum non adhaerentes facti; conceptacula magna, conica, sparsa aut in cacuminibus ramorum crebra, saepe erupta et sic depressiones in superficie relinquentia quae oram crassam elevatam interdum habent (Figura 12B). Epithallium una duabusve cellulis crassum, cellulis tholiformibus, sine incrassationibus membranae, 2–4 μm long. atque 4–8 μm diam. Meristema intercalare breve, 2–6 μm long. atque 3–7 μm diam. Perithallium plurisstratosum, gradatim plus elongatum factum (Figura 10), corpora tinctabilia et fusiones adsunt, cicatrices conceptaculorum anticedentium visibiles, cellulis 2–10 μm long. et 3–11 μm diam. Heterocystae 5–15 μm long. atque 4–11 μm diam. Hypothallium pluristratosum, coaxiale (Figura 12C), 20–250 μm crass.; cellulae 9–28 μm long. et 3–12 μm diam. Conceptacula tetrasporica uniporata, 100–320 μm super superficiem circumanbientem thalli ele-

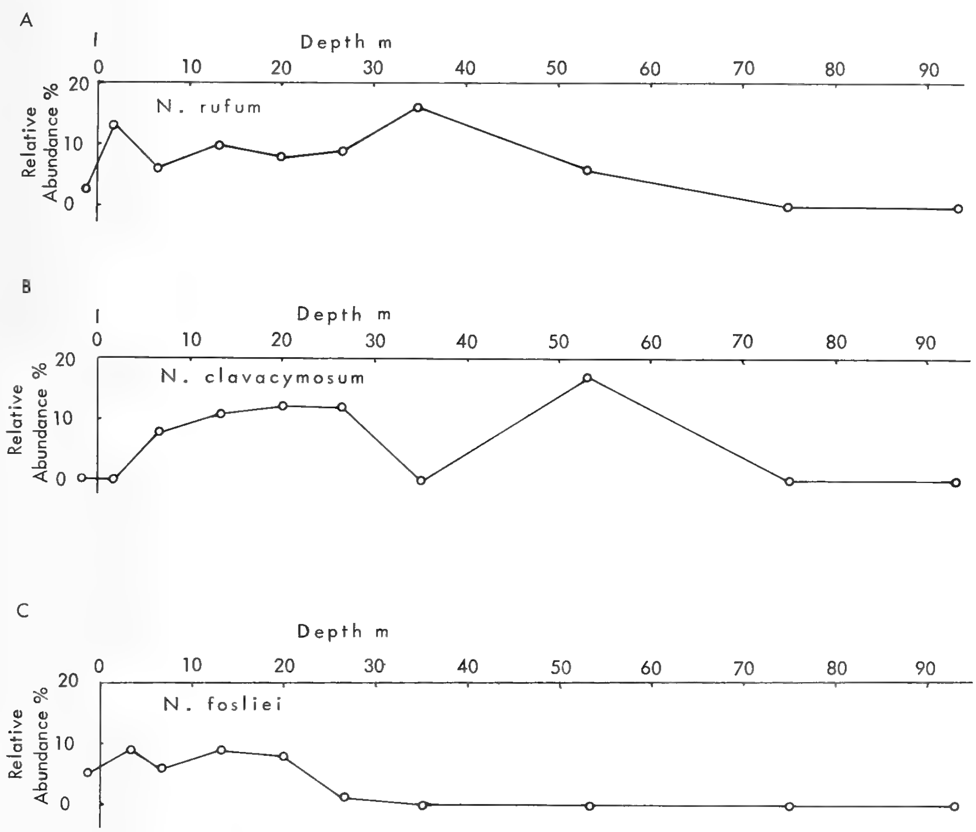


FIGURE 11.—Depth distribution: A, *Neogoniolithon rufum*, new species; B, *N. clavacymosum*, new species; C, *N. fosliei*.

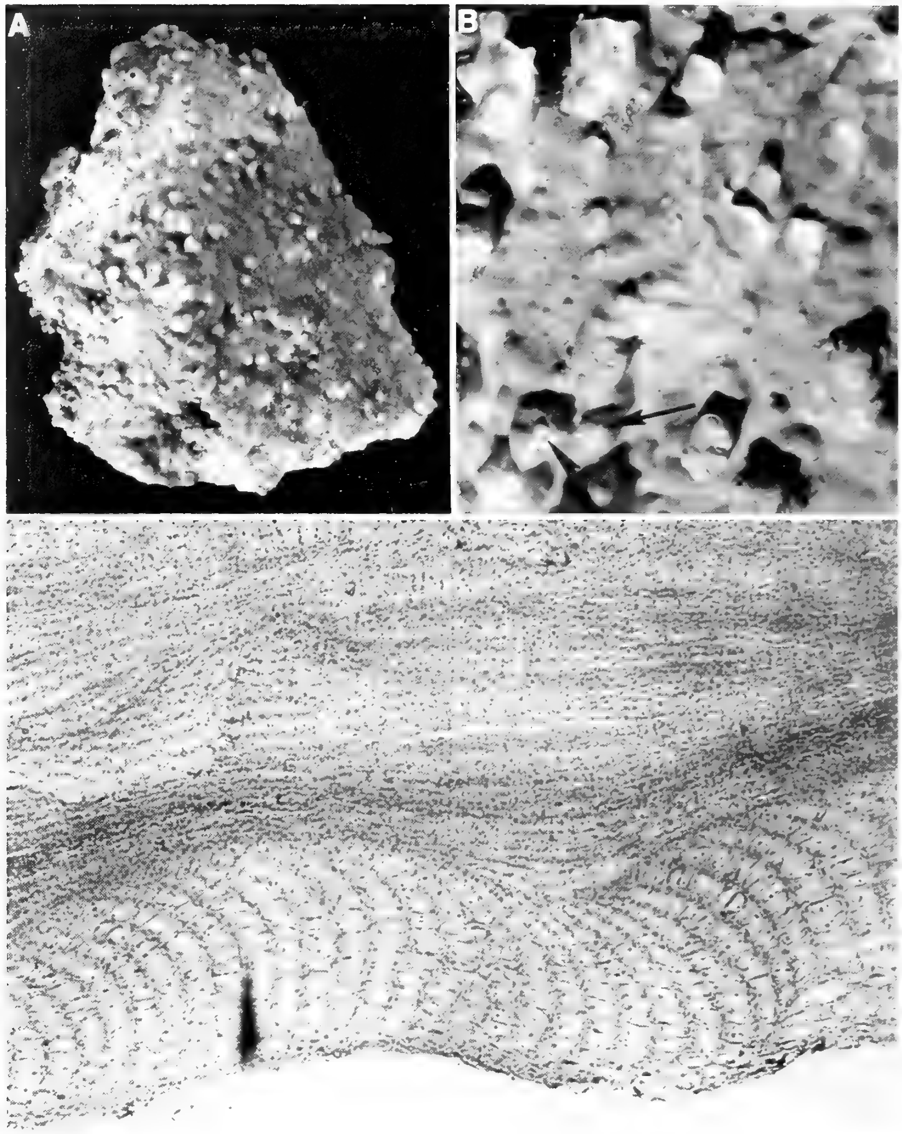


FIGURE 12.—*Neogoniolithon clavacymosum*, new species: A, habit of type specimen, × 1; B, surface of type specimen, note large uniporate conceptacles (arrow) and conceptacle scars (arrowhead), × 5; C, section showing thick coaxial hypothallium and thick zonate perithallium, × 200. (Specimen nos.: A, B, 71-58-78; C, 71-58-42.)

vata, 450–600 μm O.D., 200–500 μm I.D. atque 50–170 μm alt.; tetrasporangia ad periferiam conceptaculi restricta (columella adest), 40–90 μm long. atque 15–35 μm diam. Thalli monecii frequentes. Thalli procarpiales non visi. Conceptaculum cystocarpicum uniporatum 340 μm I.D. atque 120 μm alt.; cellula-coalescentis 230 μm diam.; carposporae solum in periferia conceptaculi repertae, 39–60 μm long. atque 25–58 μm diam. Conceptacula mascula uniporata, elevata, 310–440 μm I.D. atque 50–110 μm alt.; spermatangia ad pavimentum conceptaculi restricta; spermatia discoidea 3–5 μm diam.

Crusts well developed, becoming extensive, producing scattered short simple branches that become irregularly club shaped and often nodular

(Figure 12A,B); margins smooth and thick, becoming leafy and nonadherent to the substrate; conceptacles large, conical, scattered, or concentrated on branch tips often breaking out to leave surface depressions, sometimes having thick raised rims (Figure 12B). Epithallium 1 to 2 cells thick; cells domed, no wall thickenings, 2–4 μm long and 4–8 μm diam. Intercalary meristem short, cells 2–6 μm long and 3–7 μm diam. Perithallium multilayered, shows progressive elongation (Figure 10), staining bodies present, fusions present, scars from old conceptacles visible, cells 2–10 μm long and 3–11 μm diam. Heterocysts 5–15 μm long and 4–11 μm diam. Hypothallium multilayered, coaxial (Figure 12C), 20–250 μm thick; cells 9–28 μm long and 3–12 μm diam. Tetrasporic conceptacles unipored, raised 100–320 μm above the surrounding thallus surface, 450–600 μm O.D., 200–500 μm I.D., and 50–110 μm high; tetrasporangia restricted to the conceptacle periphery (columella present), 40–90 μm long and 15–35 μm diam. Monoecious thalli common. Procarpial thalli not seen in our collections. Cystocarpic conceptacle unipored, 340 μm I.D. and 120 μm high; fusion cell discoid 230 μm diam.; carpospores only on periphery of conceptacle, 39–60 μm long and 25–58 μm diam. Male conceptacles unipored, raised, 310–440 μm I.D. and 50–110 μm high; spermatangia restricted to the conceptacle floor; spermatia discoid 3–5 μm diam.

TYPE-LOCALITY.—Hilo Bay, Hawaii, Hawaii (19°45′N, 155°0′W), windward side of reef, 45 m depth.

HOLOTYPE.—D. Child, 71-58-78, March 1971 (USNC), Figure 12A,B.

PARATYPES.—*French Frigate:* La Perouse, August 1971, 71-78-17. *Hawaii:* Hilo Bay, March 1971, 71-58-42, 71-58-78, 71-59-36; Kawaihae, March 1971, 71-57-18. *Oahu:* Kaneohe, August 1971, 71-81-12, 71-81-24; Waianae, March 1971, 71-52-1, 71-52-3.

DISTRIBUTION.—Throughout southern Hawaiian Archipelago.

REMARKS.—The specific epithet refers to the branch shape ~~in~~ *N. clavacymosum*.

Spermatial development is similar to that described for *Paragoniolithon conicum*. Spermatangial and cystocarpic conceptacles are not buried in thallus as in *Porolithon onkodes*.

Tetrasporangial conceptacle development is similar to that described for *Paragoniolithon conicum*. Two to three tetrasporangial rows, with interspersed sterile paraphyses, are formed on the periphery of the conceptacle. A central columella of sterile paraphyses is present.

Neogoniolithon clavacymosum occurs at a frequency of about 10% throughout the shallow mid-depth range of 6–30 m (Figure 11B). The peak at 50 m (Figure 11B) is probably not real but rather a reflection of our minimal collecting in that particular zone.

In the Caribbean, *N. clavacymosum* is represented by a very similar but as yet unnamed and poorly known "pair species," which appears only sporadically in USNC Caribbean collections (Adey, unpublished data).

Neogoniolithon fosliei (Heydrich) Setchell & Mason

FIGURES 10, 11C, 13

Neogoniolithon fosliei (Heydrich) Setchell & Mason, 1943:90.—Lemoine, 1965.—Womersley and Bailey, 1970.—Gordon et al., 1976.—Zhang and Zhou, 1980.
Lithothamnion fosliei Heydrich, 1897b:58.
Lithophyllum fosliei (Heydrich) Foslie, 1897c:410.
Archaeolithothamnion fosliei (Heydrich) Foslie, 1898:4.
Goniolithon fosliei (Heydrich) Foslie, 1903a:470.—Weber-van Bosse and Foslie, 1904.—Howe, 1918b.—Setchell, 1926. [See also Lemoine, 1966, for distributional notes.]

DESCRIPTION.—Thick, extensive crusts, up to at least 5 mm thick (Figure 13A), surface dull and minutely rather rugulose, abundant large raised conceptacles dispersed evenly over surface, breaking out to leave strong scars (Figure 13A,B), often consisting of white patches or rings of dead cells; light pink on vegetative surface but attaining yellowish cast on conceptacle domes. Epithallium 2 or 3 cell layers, usually only lowest cell layer has cytoplasmic contents; cell production not synchronous, cells domed with outer tangential wall thickening of same dimensions as cell lumen, 2–

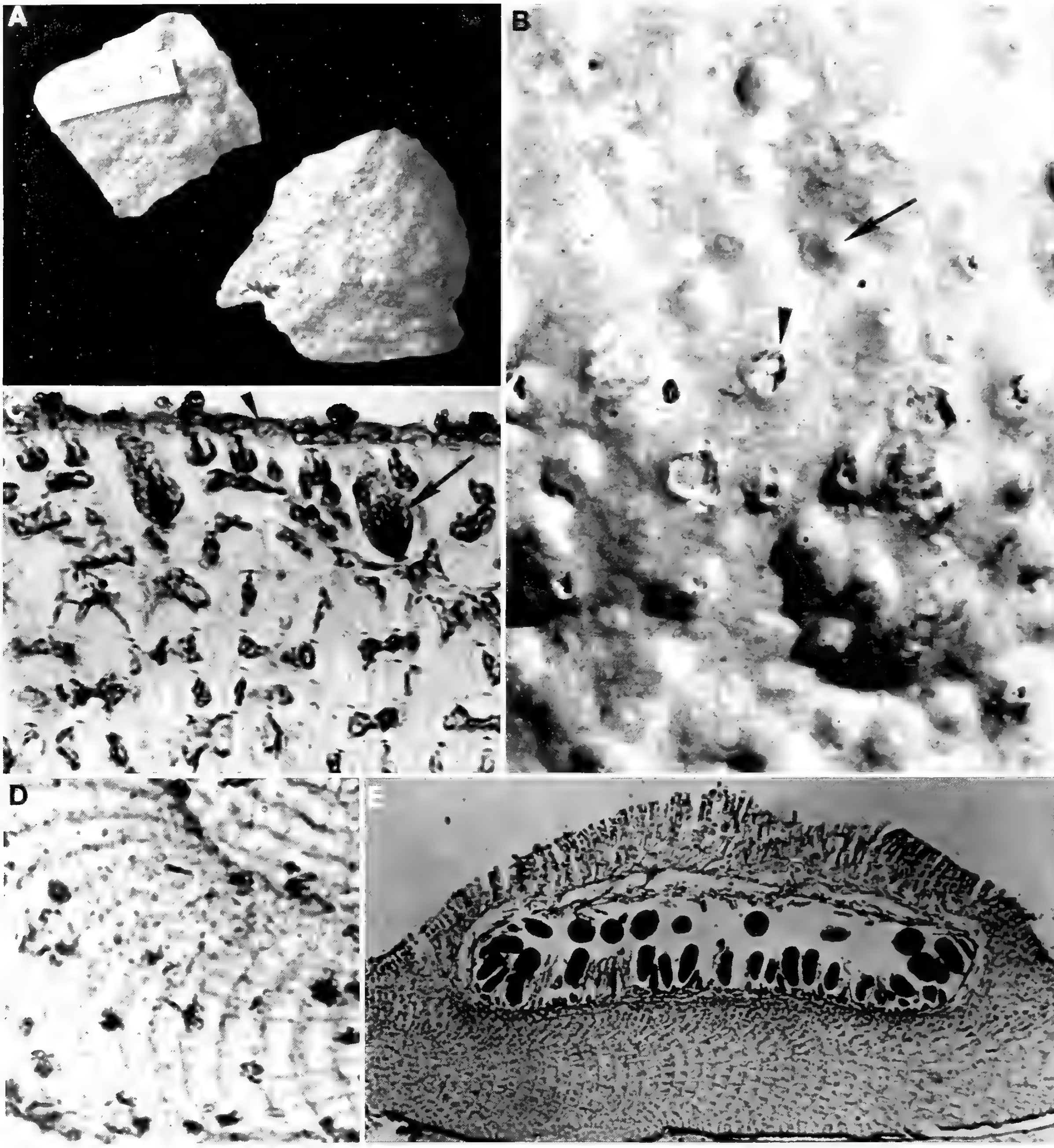


FIGURE 13.—*Neogoniolithon fosliei:* A, habit of typical specimen, × 1; B, thallus surface with conceptacles (arrow) and conceptacle scars (arrowhead), × 10; C, section through vegetative thallus, note heterocysts (arrow) and rounded epithallial cells (arrowhead), × 300; D, section through coaxial hypothallium, × 200; E, section through tetrasporangial conceptacle, × 100. (Specimen nos.: A, B, E, 71-58-47; C, D, 71-78-20.)

12 μm long and 5–13 μm diam. Intercalary meristem elongate, cells 5–29 μm long and 4–15 μm diam. Perithallial tissue irregular, little cell elongation (Figure 10), multilayered; cells 4–18 μm long and 4–15 μm diam. Heterocysts, single, large (Figure 13C), 8–49 μm long and 5–24 diam. Hypothallium parallel to coaxial, 50–200 μm thick (Figure 13D); cells 12–35 μm long and 5–19 μm diam. Tetrasporic conceptacles unipored, raised 24–300 μm above thallus, 700–1500 μm O.D., 240–900 μm I.D., and 90–190 μm high; tetrasporangia borne over entire floor, 115–160 μm long and 45–100 μm diam. (Figure 13E). No sexual conceptacles seen.

TYPE-LOCALITY.—El Tor, Red Sea.

HOLOTYPE.—Heydrich, 59, in herbarium of M. Foslie (TRH).

DISTRIBUTION.—Borneo, Guam, Maldives and Laccadives, Murray and Cocos Keeling islands, Red Sea, Solomon Islands, Tahiti, Xisha Islands.

SPECIMENS STUDIED.—*French Frigate:* La Perouse, August 1971, 71-78-20. *Hawaii:* Hilo Bay, March 1971, 71-58-23, 71-58-47. *Midway:* South Island, August 1971, 71-82-42. *Oahu:* Waikiki, March 1971, 71-50-4.

REMARKS.—*Neogoniolithon fosliei* has relatively large cells both in the meristem and the resulting perithallium, a character setting it apart from other Hawaiian members of *Neogoniolithon.* Some of the irregularity of cell size seen in Figure 10 is due to the small number of measurements. The very large and abundant heterocysts are in part responsible for the tissue irregularity. The gradual reduction of cell lumen diameter with depth in the perithallium is rather unusual among corallines, being previously described only for two crustose coralline parasites, *Ezo epiyessoense* Adey, Masaki, & Akioka and *Kvaleya epilaeve* Adey & Sperapani (Adey, Masaki, and Akioka, 1974; Adey and Sperapani, 1971), and *Mesophyllum lichenoides* Lemoine (Adey and Adey, 1973).

Neogoniolithon fosliei is a relatively shallow-water species being largely restricted to depths less than 25 m (Figure 11c). It was not found even in small quantities at depths greater than 30 m as opposed to Guam, where it has been recorded to 35 m (Gordon et al., 1976). In the Caribbean, *N. fosliei* is represented by the "pair species" *Neogoniolithon* "*megacarpum*" (nomen nudum, Adey, 1979). The latter plant is quite similar in color, anatomy, conceptacle size, and ecology, though it rarely seems to obtain the thallus thickness seen in *N. fosliei.*

Hydrolithon (Foslie) Foslie, 1909

Key to the Species

1. Thallus branched or mammillate 2
   Thallus crustose 3
2. Bluish or purplish, mammillate; large perithallial cells (mostly >12 μm long) .... ***H. reinboldii***
   Pink, simple irregular branches; small perithallial cells (mostly <12 μm long) .... ***H. breviclavium***
3. Crust thin (<200 μm), pink-yellow, conceptacles, scattered, and distinct .... ***H. laeve,*** new species
   Crust thicker (to several mm), irregular, pink, conceptacles abundant, small and not distinct .... ***H. megacystum,*** new species

Hydrolithon reinboldii (Weber-van Bosse & Foslie) Foslie

FIGURES 14–16A

Hydrolithon reinboldii (Weber-van Bosse & Foslie in Foslie) Foslie, 1909:55.—Dawson, 1954b; 1960b; 1961a.—Desikachary and Ganesan, 1966.—Littler, 1971b; 1973a,b.—Gordon et al., 1976.

Lithophyllum reinboldii Weber-van Bosse & Foslie in Foslie, 1902a:5; 1903a.

Lithophyllum cerebelloides Heydrich, 1901c:405.

Goniolithon reinboldii (Weber-van Bosse & Foslie in Foslie) Foslie in Weber-van Bosse and Foslie, 1904:49.

Porolithon reinboldii (Weber-van Bosse & Foslie in Foslie) Lemoine, 1911:166.

DESCRIPTION.—Thick well-developed tessellate crusts (Figure 14B), smooth to highly mammillate (2–10 mm diam.) (Figure 14A), red-brown when exposed to much light, light pink-lavender on shaded surfaces. Epithallium a single layer of rectangular cells, 3–5 μm long, 6–11 μm diam. Intercalary meristem slightly elongate; cells 9–14 μm long and 5–9 μm diam. Perithallium multilayered, irregular, fusions massive (Figure 14C) common deeper in the tissue; cells 5–20 μm long and 5–17 μm diam. (Figure 15). Heterocysts not abundant, single or sometimes arranged in small groups, 12–30 μm long, 9–21 μm diam (Figure 14E). Hypothallium a single layer of cells (Figure 14C,F), fusions common, cells 11–30 μm long and 5–17 μm diam. Tetrasporic conceptacles unipored, grouped, pore plugged with mucilage, conceptacle reef sunken to slightly raised (20–50 μm), 200–600 μm O.D., cavities 200–340 μm I.D. and 50–160 μm high (Figure 14D); tetrasporangia restricted to the periphery of the conceptacle (columella present), 80–100 μm long and 40–75 μm diam. No sexual material sectioned.

TYPE-LOCALITY.—Mocaras reef, inner side, east coast Borneo.

HOLOTYPE.—Weber-van Bosse, 22 June 1899, in herbarium of M. Foslie (TRH). Isotype: USNC.

DISTRIBUTION.—Borneo, El Salvador, Guam, Hawaii, India, Maldives and Laccadives, Pacific Mexico, Phillipines, Timor, Vietnam.

SPECIMENS STUDIED.—*Hawaii*: Honaunau, March 1971, 71-55-67A; Kawaihae, March 1971, 71-57-9. *Oahu*: Kaneohe, March 1971, 71-54-11, 71-54-18, 71-54-19, 71-54-21; Waikiki, March 1971, 71-50-14.

REMARKS.—A question of priority of the basionym *Lithophyllum cerebelloides* Heydrich (1901c) over *Lithophyllum reinboldii* Foslie & Weber-van Bosse in Foslie (1902a) has arisen. Both publications were available in 1901; Foslie (1902a) on 10 July 1901 (as reprints), and Heydrich (1901c) on 24 July 1901 (as a journal). Foslie 1902a was published in a volume of *Det Kongelige Norske Videnskabers Selkabs Skrifter* in 1902. Under the *International Code of Botanical Nomenclature*, article 11, *L. reinboldii* has priority over *L. cerebelloides*.

This species was sporadically abundant on shallow reef flats (0–10 m) and rubbly fore reefs throughout the Hawaiian chain. *Hydrolithon reinboldii* is sharply restricted to shallow water (Figure 16A), no specimens being found over 15 m depth. In Hawaiian waters, it is the only important shallow-water coralline alga involved in the formation of rhodoliths. See also discussion under *H. megacystum*, new species (below).

The Caribbean *Hydrolithon børgesenii* (Foslie) Foslie is quite similar to *H. reinboldii* in color, surface texture, and anatomy, though it is not usually so strongly mammillate as the Hawaiian plant. Also, *H. børgesenii* has a very wide depth range and, in the Caribbean, appears to be the ecological equivalent of all of the Pacific *Hydrolithon* species. *Hydrolithon børgesenii* is also important in the formation of shallow-water rhodoliths, though in that role it is not as abundant as the Caribbean species *Neogoniolithon mammillare* (Harvey) Setchell & Mason.

Hydrolithon breviclavium (Foslie) Foslie

FIGURES 15, 16B, 17

Hydrolithon breviclavium (Foslie) Foslie, 1909:56.—Littler, 1973b.

Goniolithon (*Hydrolithon*) *breviclavium* Foslie, 1907b:20.

DESCRIPTION.—Well-developed crusts with thick even margins adhering well to substrate, branched (Figure 17C) or mammillate (Figure 17A,B), branches short; surface similar to *Hydrolithon reinboldii* but more finely tessellate (Figure 17E), conceptacles moderately large, raised, evenly but not densely scattered over surface (Figure 17E); bright to dusty pink, deep-water plants sometimes brown. Epithallium single layered cells ellipsoidal, with thickened outer tangential wall, cells 2–10 μm long and 5–12 μm diam. Intercalary meristem cells 3.5–12 μm long and 3.5–10 μm diam. Perithallium multilayered, generally disorganized below third cell layer, fre-

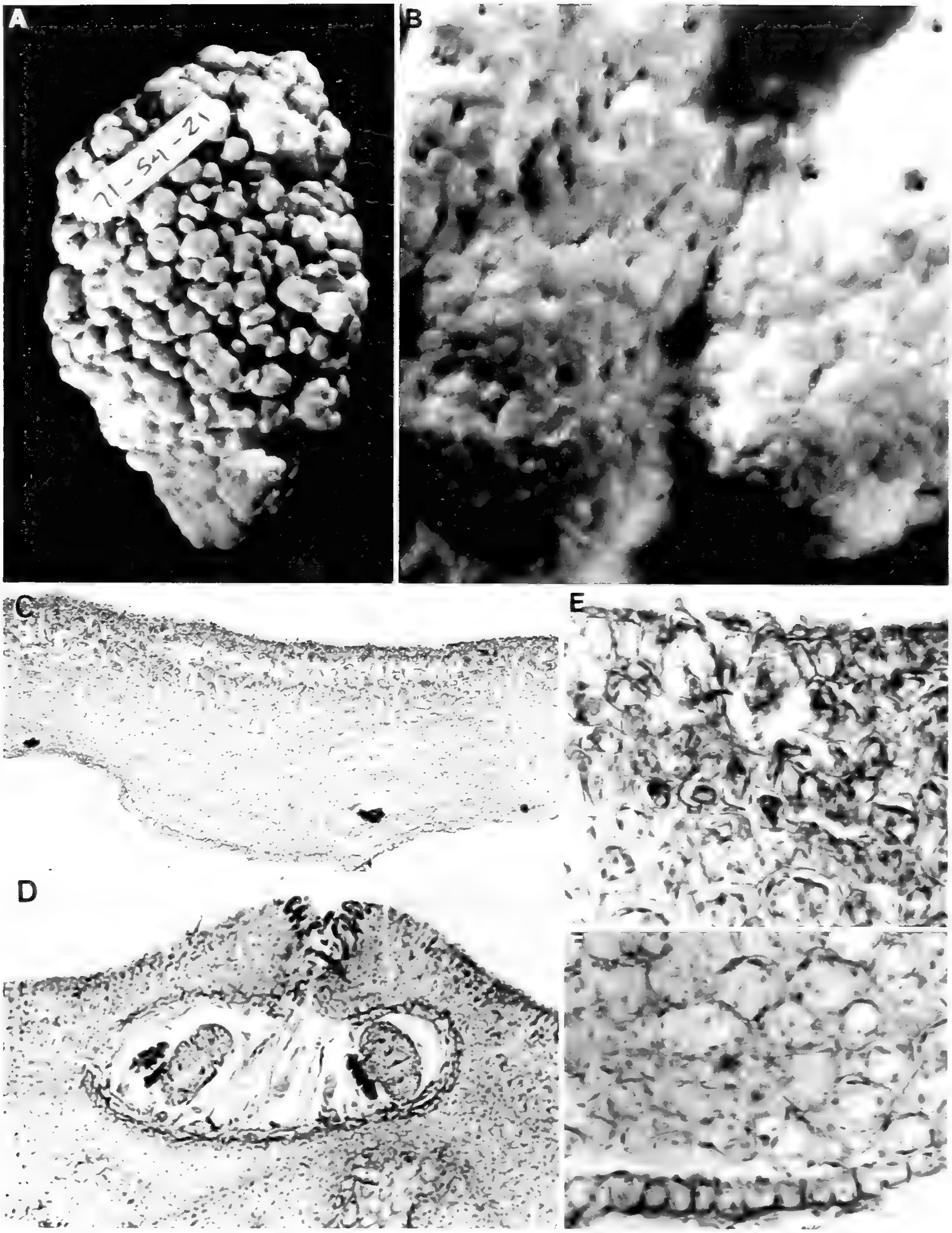


FIGURE 14.— *Hydrolithon reinboldii:* A, habit, × 1; B, surface of thallus showing conceptacles and tesselate pattern, × 10; C, transverse section through thallus, note single-layered hypothallium, × 5; D, tetrasporangial conceptacle, × 200; E, section through thallus showing heterocyst, intercalary meristem, and epithallium, × 500; F, hypothallium, × 300. (Specimen nos.: A, 71-54-21; B, 71-54-19; C, D, 71-50-14; E, F, 71-54-11; micrographs reduced to 91%.)

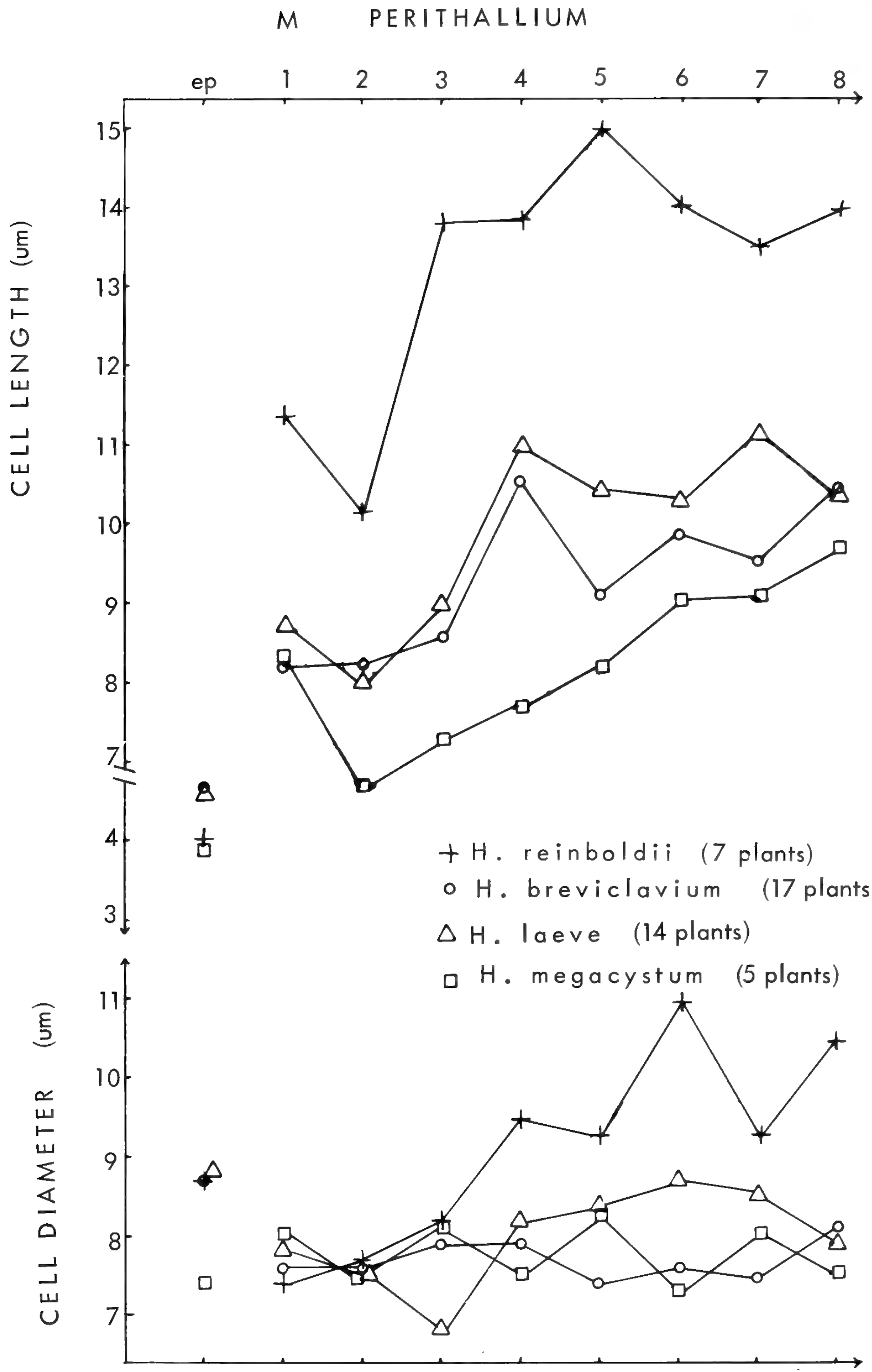


FIGURE 15.—Mean epithallial and perithallial cell dimensions in *Hydrolithon reinboldii*, *H. breviclavium*, *H. laeve*, new species, and *H. megacystum*, new species.

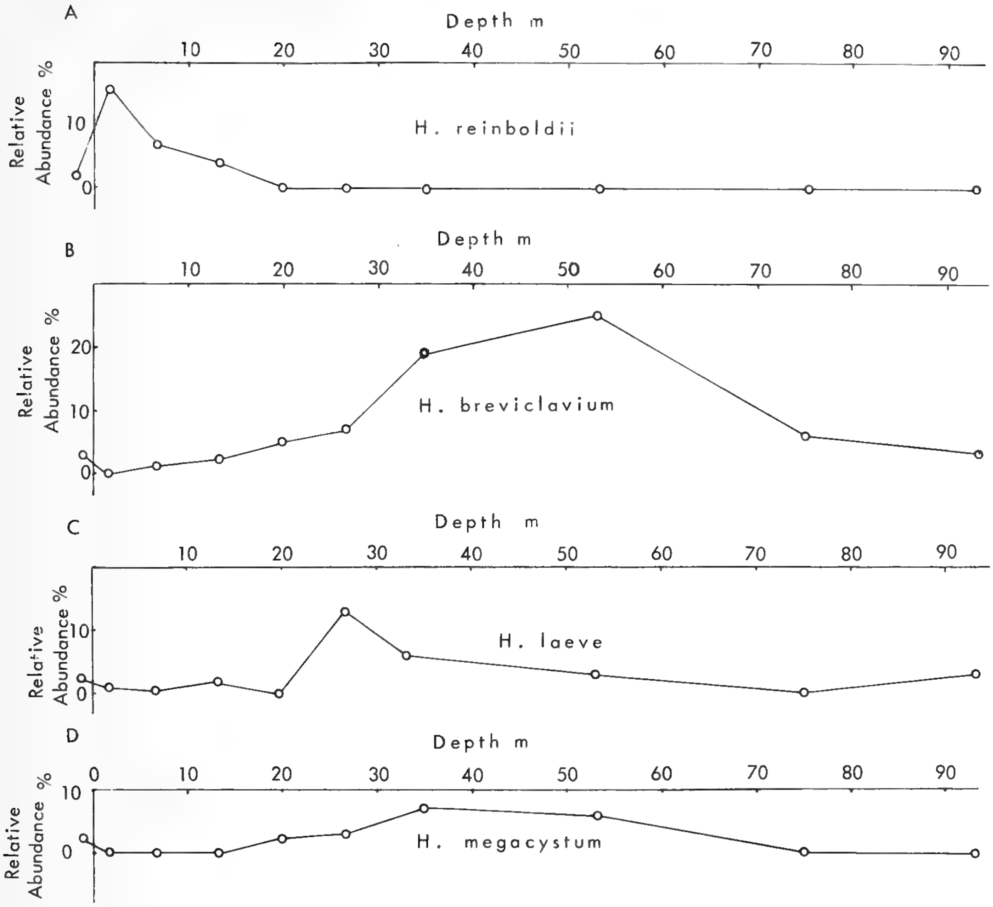


FIGURE 16.—Depth distribution: A, *Hydrolithon reinboldii;* B, *H. breviclavium*; C, *H. laeve*, new species; D, *H. megacystum*, new species.

quent wide cell fusions (Figures 15, 17F); cells 3–18 μm long and 4–13 μm diam. Heterocysts not abundant, occurring singly or in loose groups of 2 or 3, 15–36 μm long and 10–19 μm diam. Hypothallium single layer of cells (Figure 17F), 6–29 μm long and 5–18 μm diam. Tetrasporangial conceptacles unipored raised 375–1100 μm O.D., 65–180 μm high, 190–450 μm I.D.; tetrasporangia restricted to the periphery of the conceptacle, distinct columella present (Figure 17G), 70–100 μm long and 35–80 μm diam. Procarpic conceptacles single pored, raised (80–100 μm), 250–500 μm I.D., 60–130 μm high, one carpogonial branch per support cell. No cystocarpic conceptacles seen. Male conceptacles uniporate, raised (50–175 μm), 300–450 μm O.D., 150–200 μm I.D., 25–75 μm high; spermatangial branches simple, restricted to conceptacle floor; spermatia discoid, 2–4 μm diam.

TYPE-LOCALITY.—Honolulu, Hawaii.

HOLOTYPE.—Collected during *Eugenie* expedition, in herbarium of M. Foslie (TRH). Isotype: USNC.

DISTRIBUTION.—Throughout Hawaiian Archipelago.

SPECIMENS STUDIED.—*Maui*: central coast, August 1971, 71-67-4. *Molokai*: south-central, August 1971, 71-69-1. *Midway*: South Island, August 1971, 71-82-6b, 71-82-9. *Oahu*: Waikiki, March 1971, 71-50-26, 71-50-76, 71-50-78, 71-50-130. *St. Rogatiens Bank*: northwest reef, August 1971, 71-79-14, 71-79-(35-47f).

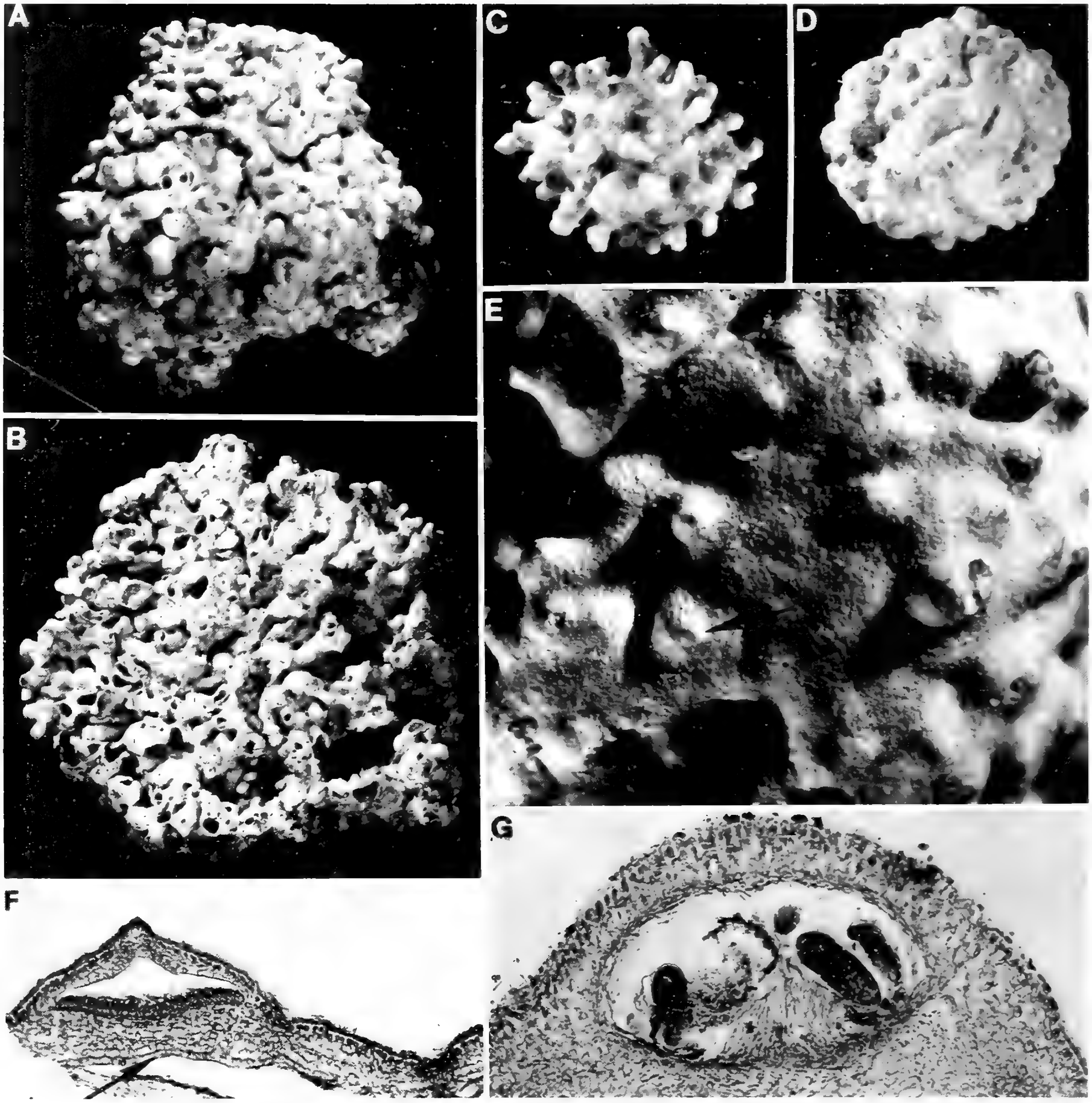


FIGURE 17.—*Hydrolithon breviclavium:* A, B, habit of mammillate thallus, × 1; C, habit of branching thallus, × 1; D, habit of nonmammillate thallus, × 1; E, surface of thallus showing tesselate appearance and conceptacles (arrow), × 5; F, section of male thallus, note single-layered hypothallium (arrow), × 300; G, section through a tetrasporangial conceptacle, × 200. (Specimen nos.: A, B, 71-50-76; C, D, 71-79-(35–47f); E, 71-50-78; F, 71-50-130; G, 71-82-6b.)

REMARKS.—Procarpic conceptacles are found buried in the thallus unfertilized; overgrowth of the conceptacles occurs from the roof of the conceptacle.

The epithallial cells in *Hydrolithon* are different from those found in *Neogoniolithon*, where tangential wall projections occur in the cell lumen. In *Hydrolithon* thickenings occur on the outer tangential wall, but there are no obvious projections.

Hydrolithon breviclavium is an abundant species

(Figure 16B) in mid to deep water (30–60 m). A few plants were found in some of the deeper dredgings at 90 m. *Hydrolithon breviclavium* is an important rhodolith former, but it tends to be overshadowed by *Lithophyllum pallescens* (Foslie) Foslie in the shallow part of its range. *Hydrolithon breviclavium* is strongly dominated by the melobesioid rhodolith formers (see "Melobesioideae") on the deep banks (50–100 m).

We do not know of a comparable Caribbean "pair species" (see discussion under *H. reinboldii*).

Hydrolithon laeve, new species

FIGURES 15, 16C, 18

DESCRIPTION.—Crustae saepe ampla, tenues (<200 μm) (Figura 18A), superficies subtilissime rugulosa (Figura 18D), colore rosaceae ad sub-

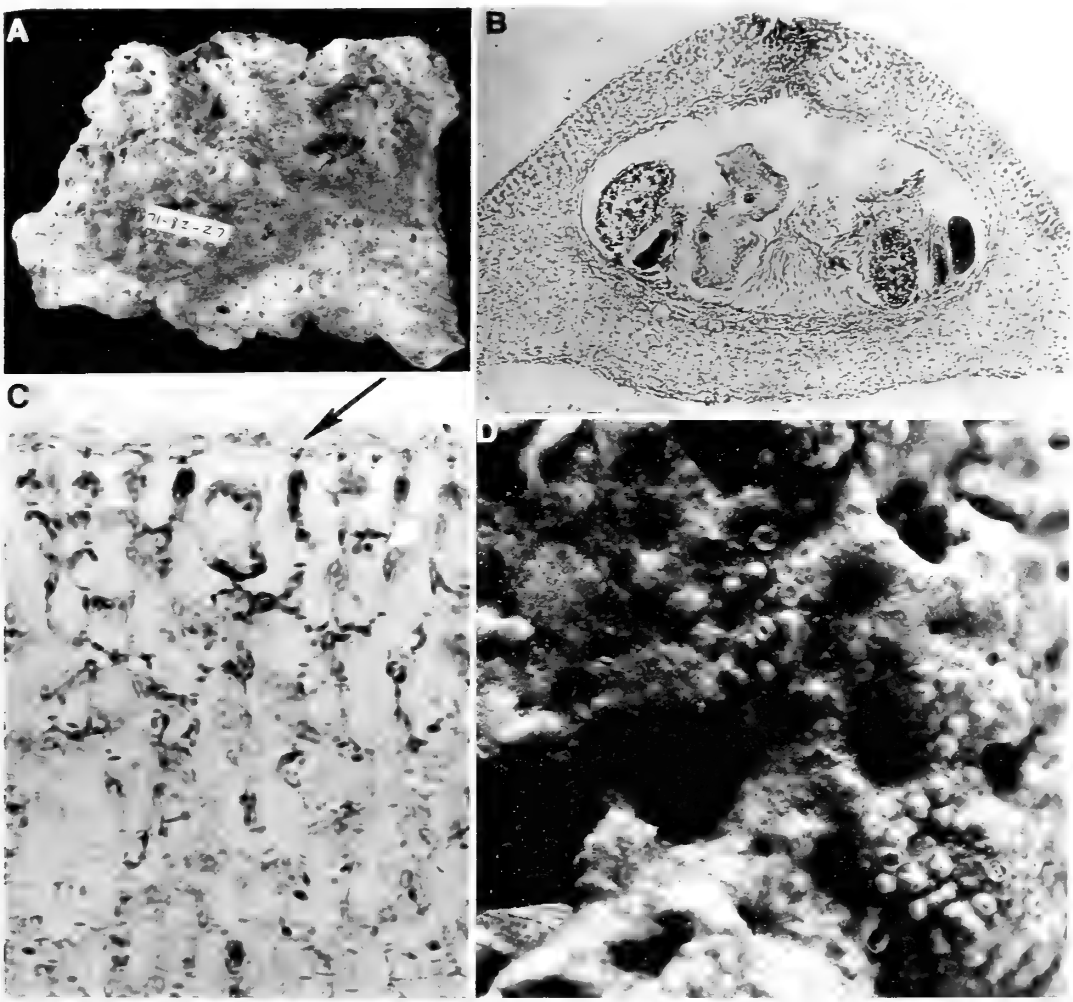


FIGURE 18.—*Hydrolithon laeve*, new species: A, habit of type specimen, × ½; B, section through tetrasporic plant, note single-layered hypothallium, tetrasporangia restricted to periphery of the conceptacle, × 200; C, section through thallus, note epithallium with outer tangential wall thickening (arrow), large single heterocyst in the perithallium, and the "large-celled" meristem, × 500; D, surface of type specimen, note tetrasporangial conceptacles, × 5. (Specimen nos.: A, D, 71-82-27; B, 71-82-24; C, 71-50-123.)

brunneas; conceptacula perspicua, elevata, sparsa magnaque praebentes (Figura 18D). Epithallium ex unico strato cellularum rotundatarum constans (Figura 18C), membrana tangentialis exterior incrassata, (3–7 μm long., 6–12 μm diam.). Meristema intercalare paululum elongatum; cellulis 6–12 μm long. atque 6–10 μm diam. (Figura 18C). Perithallium pluristratosum, irregulare, fusionibus praesentibus; cellulis 4–17 μm long. atque 4–14 μm diam., profundiores in tela maiores factae (Figura 15). Heterocystae singulae (Figura 18C) (10–25 μm long., 5–20 μm diam.) Hypothallium ex unico strato constans (Figura 18B), cellulis 9–25 μm long. atque 5–18 μm diam. Conceptacula tetrasporangialia uniporata, elevata (100–120 μm) aggregata (Figura 18B,D) (600–1100 μm O.D., 220–480 μm I.D., 90–180 μm alt.); tetrasporangia ad periferiam pavimenti conceptaculi restricta, columella adest (Figura 18B), 50–120 μm long., 30–70 μm diam. Conceptacula procarpica uniporata, elevata (80–120 μm) 500–650 μm O.D., 200–300 μm I.D., 60–120 μm alt.; omnis cellula sustinens unicum ramum carpogonialem habens.

Crusts often extensive, thin (<200 μm) (Figure 18A), surface very finely rugulose (Figure 18D), pink to brownish; scattered large, raised conspicuous conceptacles (Figure 18D). Epithallium a single layer of rounded cells (Figure 18C), wall thickening on outer tangential wall; cells 3–7 μm long, 6–12 μm diam. Intercalary meristem slightly elongate; cells 6–12 μm long and 6–10 μm diam. (Figure 18C). Perithallium multilayered, irregular, fusions present; cells 4–17 μm long and 4–14 μm diam. becoming larger deeper in the tissue (Figure 15). Heterocysts single (Figure 18C) (10–25 μm long, 5–20 μm diam.). Hypothallium a single layer (Figure 18B), cells 9–25 μm long and 5–18 μm diam. Tetrasporangial conceptacles unipored raised (100–120 μm), grouped (Figure 18B, D) (600–1100 μm O.D., 220–480 μm I.D., 90–180 μm high); tetrasporangia restricted to the periphery of the conceptacle floor, columella present (Figure 18B), 50–120 μm long, 30–70 μm diam. Procarpic conceptacles uniporate raised (80–120 μm), 500–650 μm O.D., 200–300 μm I.D., 60–120 μm high; 1 carpogonial branch per support cell. No cystocarpic or male material seen.

TYPE-LOCALITY.—Sand Island, Midway Atoll, Hawaii (28°13′N, 177°26′W). Outside reef, 27 m depth.

HOLOTYPE.—D. Child, 71-82-27, August 1971 (USNC), Figure 18A,B,D.

PARATYPES.—*Hawaii:* Honaunau, March 1971, 71-55-67b; Kawaihae, March 1971, 71-57-75. *Midway:* South Island, August 1971, 71-82-24, 71-82-26, 71-82-27. *Nihoa:* west reef, August 1971, 71-75-3. *Oahu:* Honauma, March 1971, 71-53-9; Waikiki, March 1971, 71-50-123; 71-50-132.

DISTRIBUTION.—Throughout Hawaiian Archipelago.

REMARKS.—The specific epithet *laeve* refers to its thin crustose form.

The outer tangential wall thickening of the epithallial cells of *Hydrolithon laeve* is thinner than that of *H. breviclavium.*

Hydrolithon laeve occurs as thin crusts covering the surfaces of coral and other carbonate rubble fragments. It is common from 25–50 m (Figure 16C) but may occur at any depth. We do not know of a Caribbean "pair species" (see discussion under *Hydrolithon reinboldii*).

Hydrolithon megacystum, new species

FIGURES 15, 16D, 19

DESCRIPTION.—Crustae rugulosae (Figura 19C) nodulosae (Figura 19), usque aliquot mm crass., rosaceae; conceptacula lata elevata super superficiem sparsa, interdum dense crebra (Figura 19C). Epithallium unistratosum; cellulis 3–6 μm long. atque 6–10 μm diam. Meristema intercalare non manifeste elongatum, intense tinctum potens (Figura 19B); cellulae 5–15 μm long. atque 5–10 μm diam. Perithallium pluristratosum, fusiones frequentes (Figura 19B), cellulis satis brevibus prope superficiem, profundioribus in tela, autem, progredienter longioribus factis (Figura 15) (4–16 μm long., 4–15 μm diam.). Heterocystae singulae (10–27 μm long., 7–15 μm diam.). Hypothallium unistratosum (Figura 19B); cellulis 11–29 μm

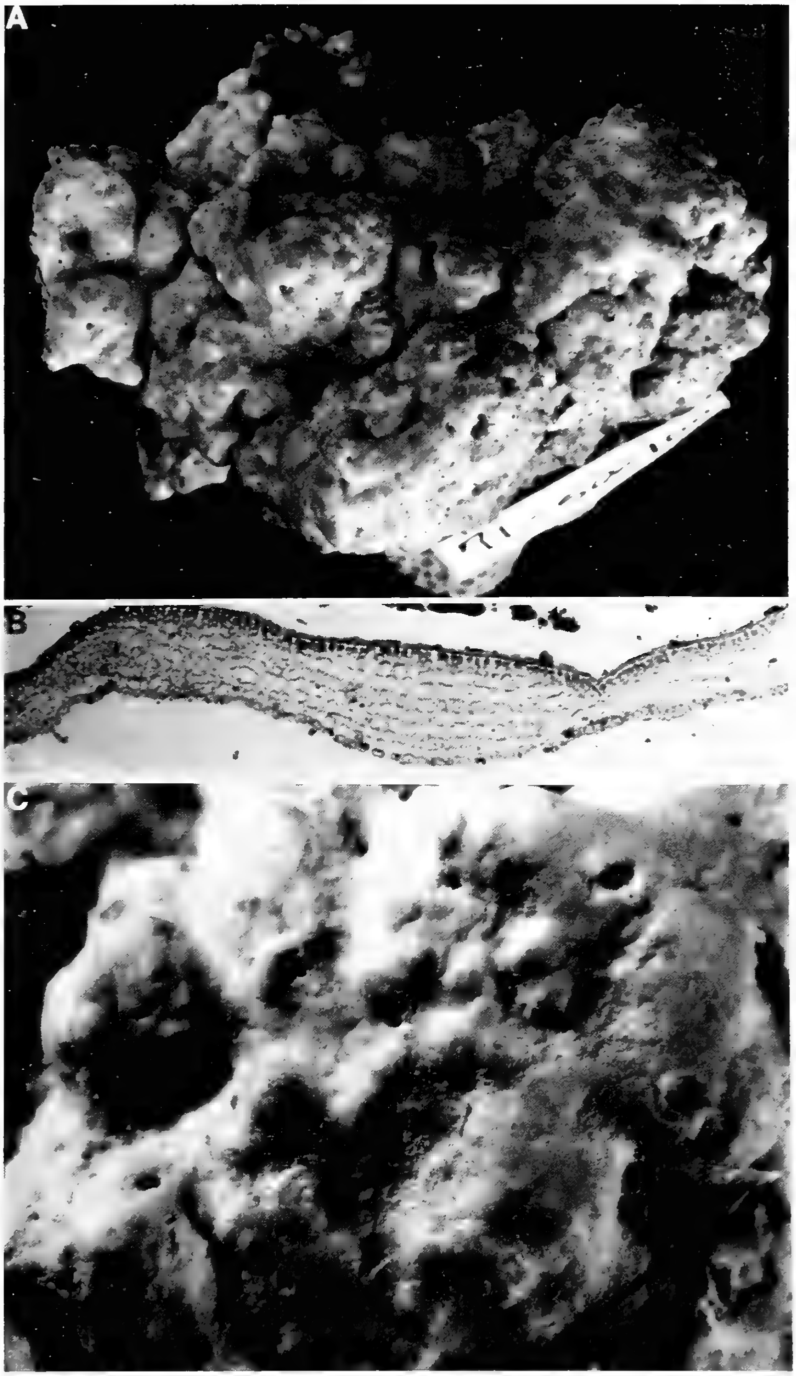


FIGURE 19.—*Hydrolithon megacystum*, new species: A, habit of type specimen, × 2; B, section through vegetative thallus, note single-layered hypothallium and heavily staining intercalary meristem, × 50; C, surface of type specimen showing conceptacles, × 10. (Specimen nos.: A, C, 71-50-100; B, 71-82-3.)

long. atque 6–15 μm diam. Conceptacula tetrasporangialia uniporata, lata, elevata (150–200 μm), 400–800 μm O.D., cavitates 300–440 μm I.D. atque 100–240 μm alt., paraphyses steriles adsunt; tetrasporangia trans totum pavimentum conceptaculi disposita, 75–170 μm long., 30–100 μm alt.

Crusts rugulose (Figure 19c), nodular (Figure 19a) becoming several mm thick, pink; broad raised conceptacles scattered over surface, occasionally densely concentrated (Figure 19c). Epithallium a single layer; cells 3–6 μm long and 6–10 μm diam. Intercalary meristem not markedly elongate, stains heavily (Figure 19b); cells 5–15 μm long and 5–10 μm diam. Perithallium multilayered, fusions common (Figure 19b), cells quite short near surface but becoming progressively elongate with depth in the tissue (Figure 15) (4–16 μm long, 4–15 μm diam.). Heterocysts single (10–27 μm long, 7–15 μm diam.). Hypothallium a single layer of cells (Figure 19b); cells 11–29 μm long and 6–15 μm diam. Tetrasporangial conceptacles uniporate, broad, raised (150–200 μm), 400–800 μm O.D., cavities 300–440 μm I.D. and 100–240 μm high, sterile paraphyses present; tetrasporangia across entire floor of conceptacle, 75–170 μm long, 30–100 μm high. No sexual material seen.

Type-Locality.—Waikiki, Oahu, Hawaii (21°16′N, 157°50′W), leeward.

Holotype.—D. Child, 71-50-100, March 1971 (USNC), Figure 19a.

Paratypes.—*Hawaii:* Hilo Bay, March 1971, 71-58-68. *Maui:* south-central coast, August 1971, 71-66-14. *Midway:* South Island, August 1971, 71-82-3. *Oahu:* Waikiki, March 1971, 71-50-100.

Distribution.—Throughout Hawaiian Archipelago.

Remarks.—The specific epithet *megacystum* refers to the unusually large reproductive structures.

Hydrolithon breviclavium, *H. megacystum*, and *H. laeve* range widely in the mid-depth zones (Figure 16b,c,d), although *H. breviclavium* is twice as common as the other two species. *Hydrolithon laeve* does not contribute to rhodolith formation, though *H. megacystum* may occasionally occur in this form. These three species are not known in the Indo-Pacific outside of Hawaii. This is probably not indicative of actual occurrence, since corallines have not been widely collected and identified from the subtidal beyond Hawaii; the *Siboga* expedition (Weber, 1902) dredging was generally in deeper water. Some reports of *H. reinboldii* may actually belong to our new species.

All of the four *Hydrolithon* species have elongate intercalary meristems and considerable additional cell elongation with burial in the perithallium (Figure 15). Perithallial cell elongation is quite rapid in *H. reinboldii* but more gradual in the other three species which occupy roughly the same depth range and are probably closely related; it would be of considerable interest to examine the microhabitat preferences of these species.

Lithoporella (Foslie) Foslie, 1909

Lithoporella melobesioides (Foslie) Foslie

Figure 20

Lithoporella melobesioides (Foslie) Foslie, 1909:59.—Lemoine, 1963.—Masaki, 1968.—Papenfuss, 1968.—Womersley and Bailey, 1970.—Gordon et al., 1976.

Mastophora melobesioides Foslie, 1903b:24; 1908a,b.—Weber-van Bosse and Foslie, 1904.

Description.—Thin, usually leafy, pink to maroon crusts with scattered raised conceptacles (Figure 20a,b,c), growth fanlike and easily discernible under the dissecting microscope (Figure 20b). Epithallium a single cell layer; cells rounded to triangular (Figure 20d), 3–5 μm long, 7–8 μm diam. Perithallium present only around conceptacles, lateral fusions common, no secondary pit connections (Figure 20d); cells 4–14 μm long and 7–11 μm diam. Hypothallium single layered, fusions absent; cells 30–40 μm long and 10–15 μm diam. Tetrasporangial conceptacles unipored, highly raised, 600–1200 μm O.D. No sexual material seen.

TYPE-LOCALITY.—Maldive Islands, Nilandu Atoll, Indian Ocean.

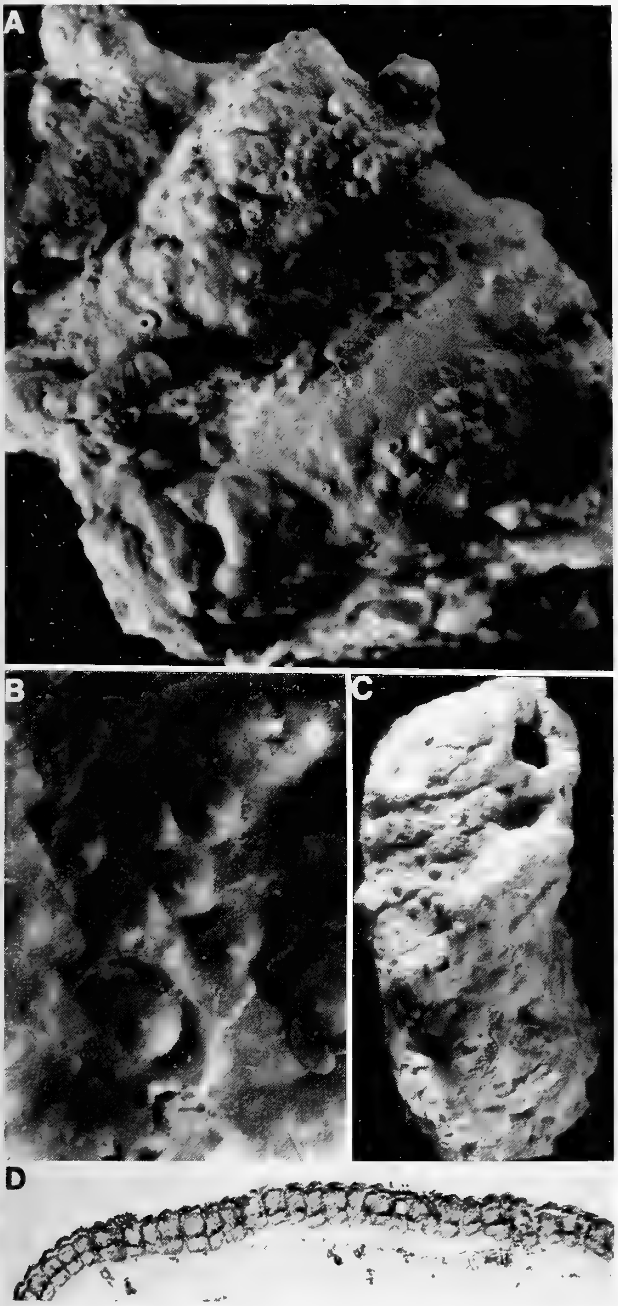


FIGURE 20.—*Lithoporella melobesioides:* A, surface of thallus showing tetrasporangial conceptacles and "fan-like" overgrowth, × 2; B, surface of thallus showing large-celled overgrowth patterns, × 10; C, habit, × 1; D, section through vegetative thallus, × 10. (Specimen nos.: A–C, 71-59; D, 71-81-16.)

HOLOTYPE.—Gardiner, 20 April 1900, 36 fathoms, in herbarium of M. Foslie, (TRH). Isotype: USNC.

DISTRIBUTION.—Borneo, Cape Verde Island, Guam, Japan, Java, Philippines, Red Sea, Samoa, Solomon Islands, Timor.

SPECIMENS STUDIED.—*Molokai:* southwest coast, August 1971, 71-73-8, *Oahu:* Hilo, March 1971, 71-59; Honauma, March 1971, 71-53-6; Kaneohe, March 1971, 71-81-16.

REMARKS.—We found nine specimens of *Lithoporella*; all were referred to *L. melobesioides* (Foslie) Foslie. *Lithoporella* is found from the intertidal to 85 m depth and from Midway Atoll to the island of Hawaii. Only three specimens were microtome-sectioned; therefore, the preceding description is minimal. Considering the wide depth range of *Lithoporella* it is possible that we mixed several species. A more detailed study is therefore desirable.

LITHOPHYLLOIDEAE Setchell, 1943

Tenarea Bory, 1832

Only one species is recognized in the Hawaiian flora.

Tenarea tessellatum (Lemoine) Littler

FIGURES 21, 22

Tenarea tessellatum (Lemoine) Littler, 1971a:355.
Lithophyllum (*Dermatolithon*) *tessellatum* Lemoine, 1929:68.—Taylor, 1945.
Goniolithon tessellatum (Lemoine) Setchell & Mason 1943:89.—Dawson, 1960b.

DESCRIPTION.—Glossy, thin to several mm thick, bright pink to reddish crusts showing a very distinctive concentric or spiral pattern of overlapping tissue layers with thin white growth margins (Figure 21A,C), "terraces" varying from 200–2000 μm in width, scattered broad but slightly raised conceptacles that leave circular depressions or are covered by the overlapping growth (Figure 21A,D). Thallus 2 cell layers; up-

per cell layer (epithallium) triangular or rounded, cells 2–8 μm long and 5–13 μm diam.; lower cell layer (hypothallium), cells 30–50 μm long and 7–15 μm diam. Tetrasporangial conceptacles unipored, initially raised (90–110 μm) but quickly buried by overlapping growth (Figure 21B,D), conceptacles 500–700 μm O.D., 210–430 μm I.D., and 70–180 μm high (Figure 21B); tetrasporangia restricted to the periphery of the conceptacle, columella present, 50–100 μm long and 30–50 μm diam. One female plant seen, cystocarpic conceptacles, unipored, raised 400 μm O.D., 210–250 μm I.D., 70–80 μm high, not buried in thallus; carposporangia restricted to periphery of large discoid fusion cell; fusion cell, 125 μm diam.; carpospores rounded, 30–35 μm diam. No male conceptacles seen.

TYPE-LOCALITY.—Post Office Bay, Floreana (Charles) Island, Galapagos Islands.

HOLOTYPE.—Crossland, s.n., August 1924 (PC).

DISTRIBUTION.—Galapagos, Hawaii, Panama.

SPECIMENS STUDIED.—*Hawaii:* Honaunau, March 1971, 71-55-26. *Midway:* Lagoon, March 1971, 71-62-40; South Island, August 1971, 71-82-22, 71-82-59. *Oahu:* Honauma, March 1971, 71-53-18; Waikiki, March 1971, 71-50-44, 71-50-89.

REMARKS.—The specific epithet *tessellatum* describes a mozaic pattern rather than the spiral pattern seen on the thallus surface of *T. tessellatum*. It is unfortunate Lemoine (1929:68) chose this name, since confusion with the "tessellate surface" of *Hydrolithon reinboldii* may occur.

Tenarea tessellatum was fairly common in our collections from the intertidal to 40 m depth (Figure 22). The Caribbean alga *Tenarea prototypum* (Foslie) Adey is a "pair species" of *T. tessellatum*. It is common in the Caribbean (Adey, 1979) and appears to differ from *T. tessellatum* by having much narrower "terraces" (rarely more than about 1 mm wide).

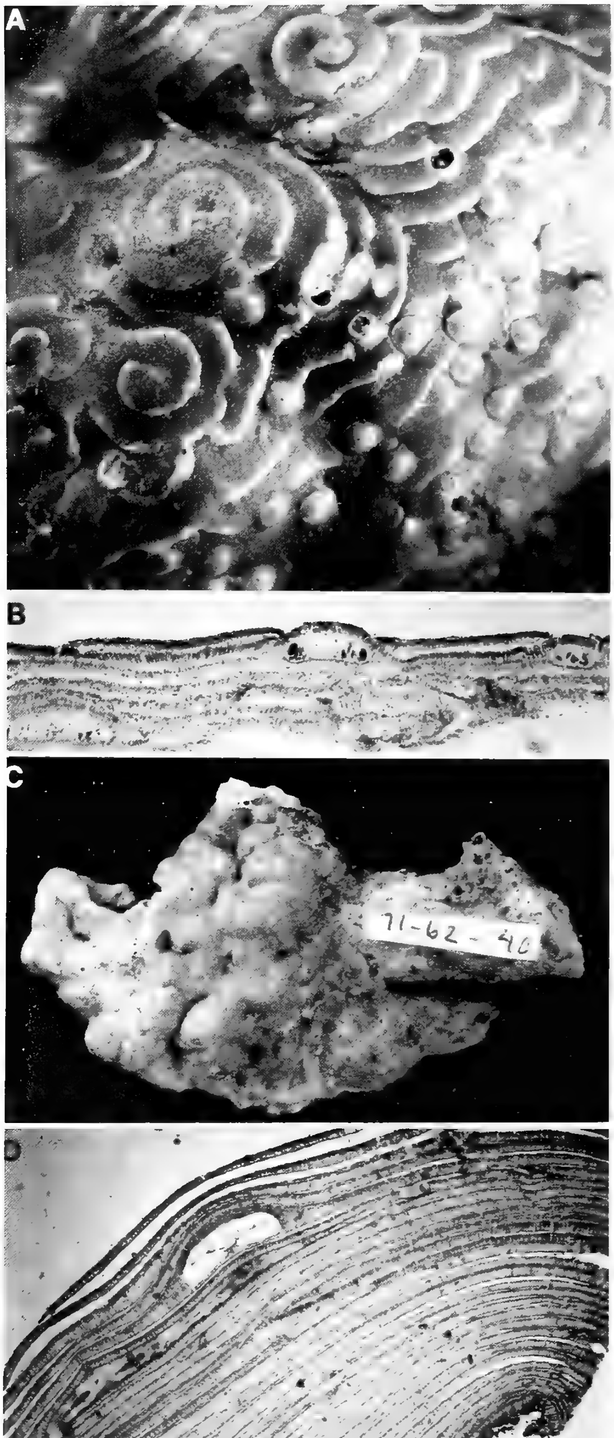


FIGURE 21.—*Tenarea tessellatum:* A, surface of thallus showing spiral "terraces" and tetrasporangial conceptacles, × 10; B, section through thallus showing tetrasporangial conceptacles (arrowed), × 50; C, habit, × 1; D, section through thallus showing overgrowth of conceptacles, × 50. (Specimen nos.: A, C, 71-62-40; B, 71-82-59; D, 71-50-89; micrographs reduced to 90%.)

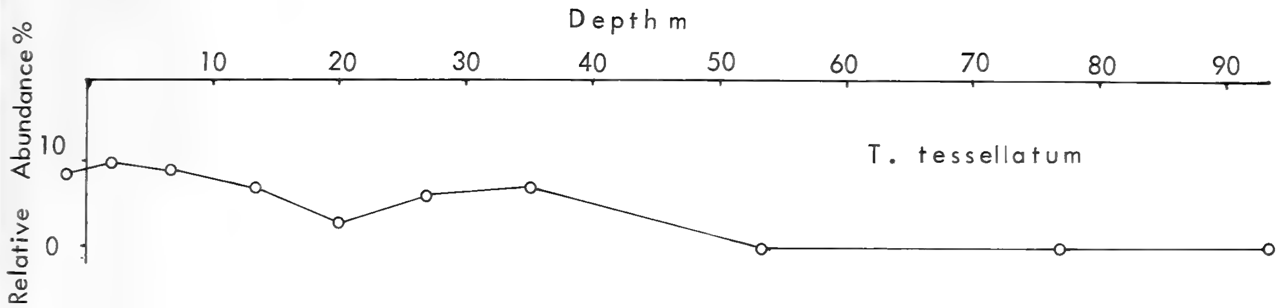


FIGURE 22.—Depth distribution of *Tenarea tessellatum.*

Lithophyllum Philippi, 1837

Key to the Species

1. Plants branched 2
   Plants crustose 3
2. Branches long, terete to flattened .... ***L. kotschyanum***
   Branches short, terete to mushroom shaped .... ***L. pallescens***
3. Crust tessellate .... ***L. insipidum,*** new species
   Crust smooth 4
4. Crust smooth glossy, pink, medium-sized conceptacles (>300 μm O.D.) .. .. ***L. ganeopsis,*** new species
   Crust smooth dull, pink, very small conceptacles (<200 um O.D.) .... ***L. punctatum***

Lithophyllum kotschyanum Unger

FIGURES 23–25

Lithophyllum kotschyanum Unger, 1858:22.—Foslie, 1909; 1929.—Pilger, 1919.—Gordon et al., 1976.
Lithothamnium kotschyanum Unger, 1858:22.
[See also synonyms listed by Foslie, 1909, 1929.]

DESCRIPTION.—Massive branching plants, sometimes with an extensive basal crust (Figure 24B) but most commonly densely branched with little crust; wide range of branch morphology: short simple knobs, long thin finger-like projections, vertical plates or large fused clubs (Figure 24A,B,C,D); glossy; red-purple, frequently becoming white and chalky on enlarged branch ends; conceptacles slightly raised with no definite borders, densely grouped when present (Figure 24D) but often completely absent. Epithallium single cell layer, often absent; cells 2–4 μm long and 6–12 μm diam. Intercalary meristem generally elongate, forming a distinct layer; cells 5–25 μm long and 7–11 μm diam. Perithallium multilayered; cells often arranged in horizontal layers of uniform size and alignment (Figure 24E,F) elongating greatly with branching or change in direction of growth, secondary pit connections common (Figure 24F), 4–24 μm long and 4–10 μm diam. (Figure 23). Hypothallium single layer, lower perithallium often curved upwards into false coaxial hypothallium; cells isodiametric to slanting palisade, size varying greatly, 6–21 μm long and 7–25 μm diam. Tetrasporangial conceptacles unipored, usually level with surface or slightly raised (occasionally raised to 60 μm), 350–450 μm O.D., 250–370 μm I.D., 80–210 μm high, raised central columella present (Figure 24E); tetrasporangia

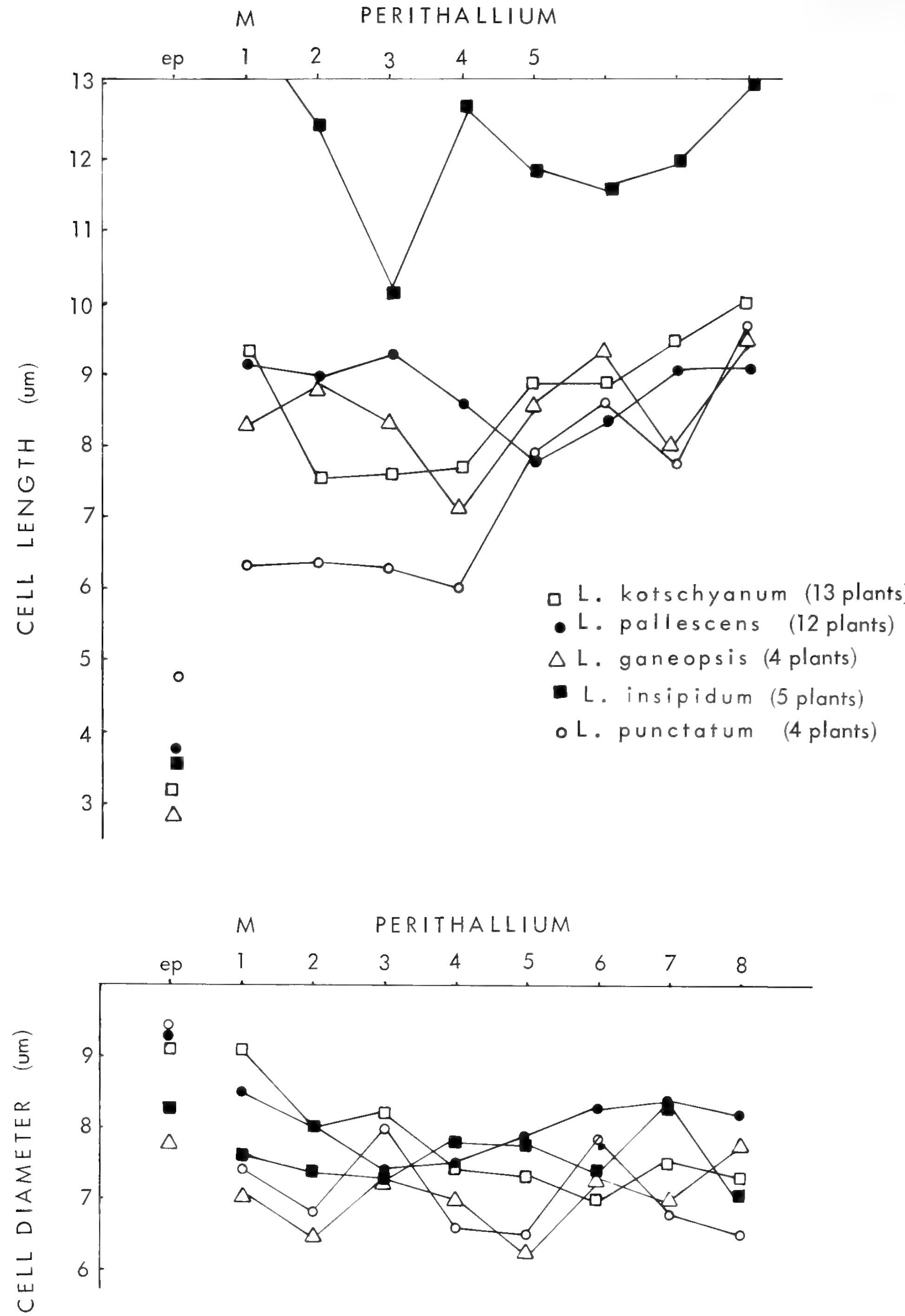


FIGURE 23.—Mean epithallial and perithallial cell dimensions of *Lithophyllum kotschyanum*, *L. pallescens*, *L. ganeopsis*, new species, *L. insipidum*, new species, and *L. punctatum*.

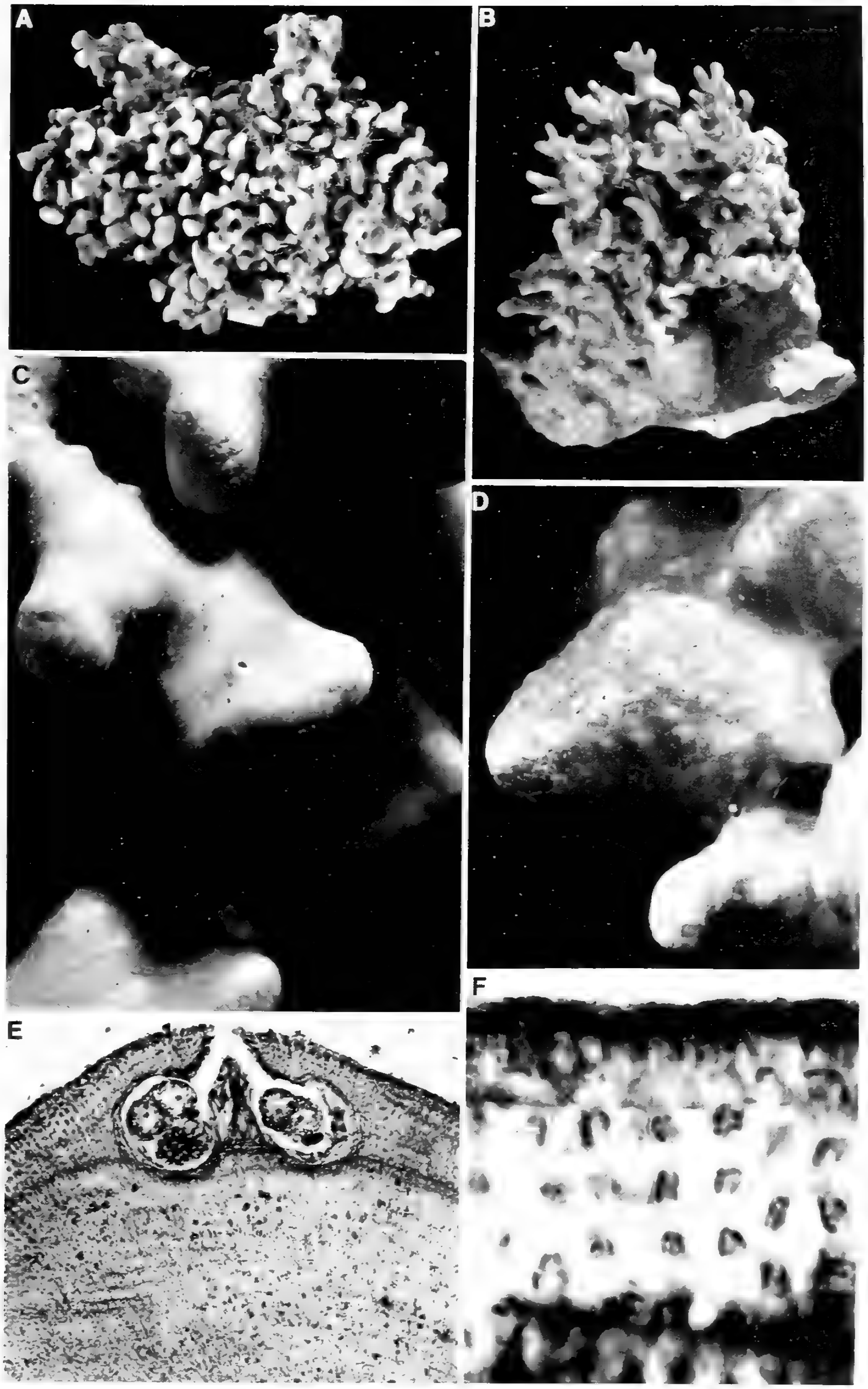


FIGURE 24.—*Lithophyllum kotschyanum*: A, B, habit, × 1; C, close-up of branches, × 10; D, surface with conceptacles, × 10; E, tetrasporangial conceptacle showing raised central columella, × 130; F, perithallium with secondary pit connections, × 500. (Specimen nos.: A, C, 71-57-12; B, 71-57-2; D, 71-59-10; E, 71-57-1; F, 71-59-8; micrographs reduced to 80%.)

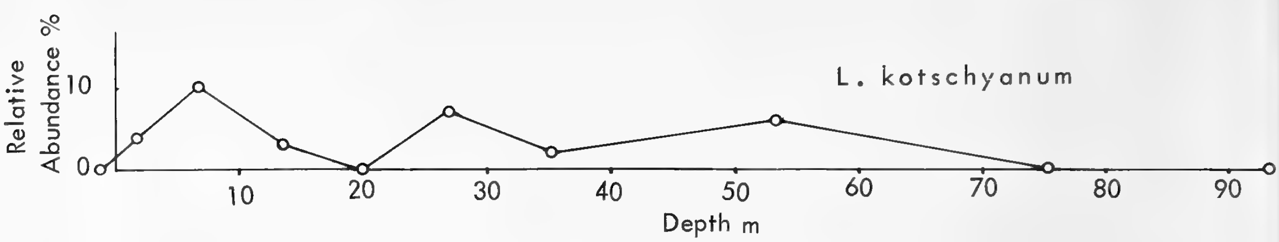


FIGURE 25.—Depth distribution of *Lithophyllum kotschyanum*.

and bisporangia restricted to the conceptacle periphery, 40–100 μm long, 20–60 μm diam. No sexual material was found.

TYPE-LOCALITY.—Gulf of Bahrain, Persian Gulf.

HOLOTYPE.—Kotschy, in herbarium of M. Foslie (TRH). Isotype: USNC.

DISTRIBUTION.—Guam, Persian Gulf, Red Sea.

SPECIMENS STUDIED.—*Hawaii:* Hilo Bay, March 1971, 71-58-72, 71-59-8, 71-59-10, 71-59-25; Honaunau, March 1971, 71-56-1; Kawaihae, March 1971, 71-54-1, 71-57-2, 71-57-12. *Midway:* lagoon, March 1971, 71-62-21; South Island, August 1971, 71-82-60. *Oahu:* Kaneohe, August 1971, 71-82-60.

REMARKS.—*Lithophyllum kotschyanum* is similar in habit, surface detail, and morphology anatomy to the Caribbean alga *Lithophyllum congestum* (see Steneck and Adey, 1976), yet there are some differences in the ecology of these plants. In the Caribbean, *L. congestum* is an algal ridge builder, the peak of its abundance occurring at mean low water. At depths of several meters, the branches are much reduced, and the few plants found at 5–10 m are generally without branches. On the other hand, *L. kotschyanum* occurs to a considerable depth in Hawaii (Figure 25) and, at least in our data, was much less abundant at low water levels, although Littler (pers. comm.) indicates *L. kotschyanum* replaces *P. gardineri* to some extent on the algal ridges, especially along channel and groove sides.

Lithophyllum pallescens (Foslie) Foslie

FIGURES 23, 26, 27

Lithophyllum pallescens (Foslie) Foslie, 1900c:20; 1901a; 1909.—Dawson, 1944; 1954a; 1960b; 1961b.—Heydrich, 1901a.—Lemoine, 1911.

Lithothamnion pallescens Foslie, 1895:4.—Heydrich, 1897b,c.

Goniolithon pallescens (Foslie) Foslie, 1898:9.

Lithophyllum okamurai Foslie, 1900b:4; 1904; 1906.—Weber-van Bosse and Foslie, 1904.—Howe, 1918b.—Okamura, 1936.—Masaki and Tokida, 1963.—Lemoine, 1965; 1966.—Masaki, 1968.—Papenfuss, 1968.—Womersley and Bailey, 1970.

Lithophyllum californiense Heydrich, 1901a.

Lithophyllum cephaloides Heydrich, 1901b:271.

DESCRIPTION.—Plants initially crustose but quickly developing densely spaced small short simple club-shaped branches (Figure 27A,B); initial growth usually occurs on attached substrate, but a developed head often becomes detached and occasionally forms large rhodoliths reaching to 8 cm diam. (Figure 27A); surface fairly smooth with occasional patches of small light-colored conceptacles, slightly raised or sometimes slightly depressed. Cover cells present. Epithallium usually a single cell layer (rarely 2 cell layers); cells 2–7 μm long and 7–12 μm diam. Intercalary meristem a distinct layer; cells usually quite square but occasionally elongating individually, 5–15 μm long and 6–11 μm diam. Perithallium multilayered, regular with strong horizontal layering secondary pit connections common between cells; cells 5–18 μm long and 4–15 μm diam. (Figure 23). Hypothallium single layer when present (Figure 27C); cells 6–24 μm long and 6–10 μm diam. Tetrasporangial conceptacles unipored, usually level with surface (may be sunken (20 μm) or raised (5 μm)) 140-310 μm I.D., 50-160 μm high; tetrasporangia restricted to the periphery of conceptacle (columella present), 30–45 μm long and 15–20 μm wide. Male conceptacle uniporate, raised (70–100 μm) 190–480 μm I.D., 30–80 μm high; spermatangial mother cells restricted to the conceptacle floor, 2 spermatial extensions

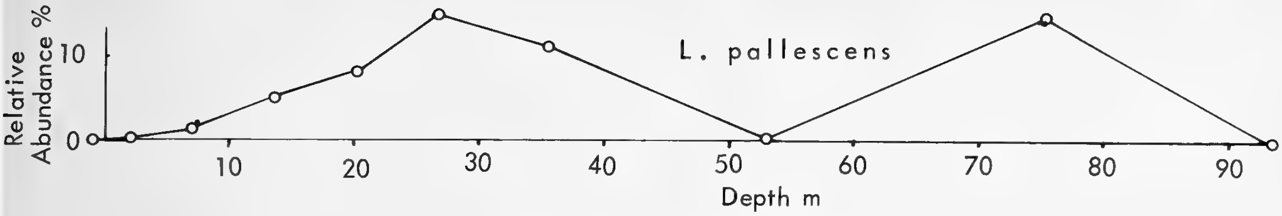


FIGURE 26.—Depth distribution of *Lithophyllum pallescens.*

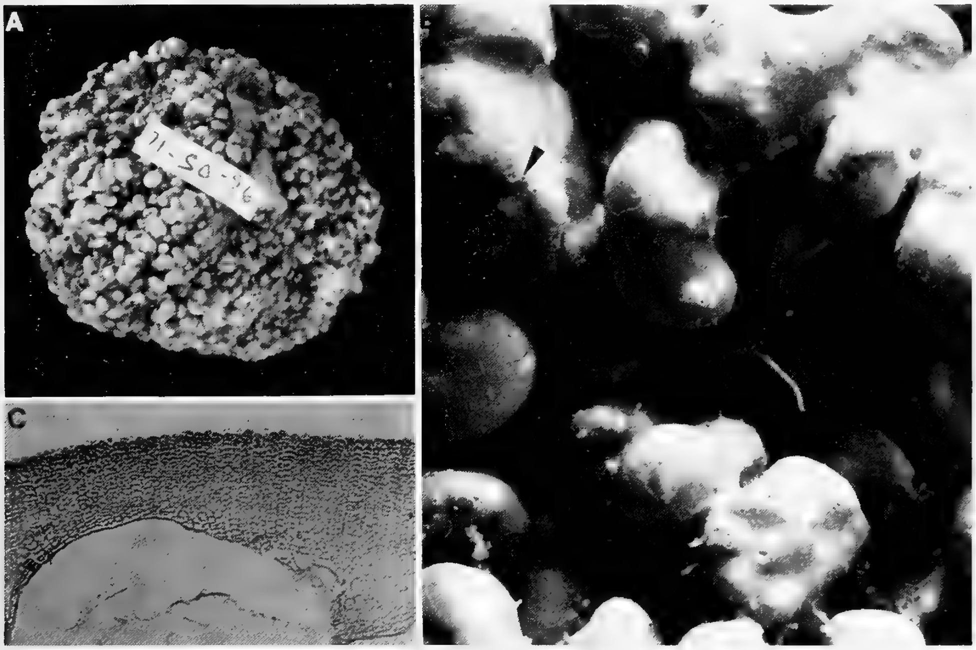


FIGURE 27.—*Lithophyllum pallescens:* A, habit of typical rhodolith, × 1; B, surface showing branches and conceptacles (arrowhead), × 10; C, section through vegetative thallus, × 100. (Specimen nos.: A–C, 71-50-96; micrographs reduced to 81%.)

per mother cell; spermatia discoid, wound into mucus strands in conceptacle cavity, 1–2 μm diam.

TYPE-LOCALITY.—Sublittoral bank along the west shore of Isla Espiritu Santo, near La Paz, Gulf of California, Mexico.

HOLOTYPE.—Diguet Hariot #5, in the herbarium of M. Foslie (TRH). Isotypes: PC, UC.

DISTRIBUTION.—Australia; Baja, California; Borneo, Gulf of California, Indian Ocean, Japan, New Guinea, Panama, Phillipines, Red Sea, Solomons, Vietnam.

SPECIMENS STUDIED.—*Hawaii:* Hilo, March 1971, 71-58-53; Honaunau, March 1971, 71-55-20. *Midway:* lagoon, March 1971, 71-62-33. *Molokai:* southwest, August 1971, 71-73-9. *Oahu:* Kaneohe, March 1971, 71-54-2, August 1971, 71-81-34; Waikiki, March 1971, 71-50-52, 71-50-96.

REMARKS.—We have been unable to differentiate between *Lithophyllum okamurai* Foslie (1900), the designation usually used for Indo-Pacific specimens of this plant (see Womersley and Bailey, 1970), and *L. pallescens.* Since *L. pallescens* has priority by five years, we use that name here.

The outside diameter of tetrasporangial conceptacles has not been given since such a measurement has little taxonomic value in *Lithophyllum pallescens.* The development of the male con-

ceptacle is similar to that described for *Paragoniolithon conicum.*

Lithophyllum pallescens is a primary rhodolith-builder in depths of 15–80 m (the low value at 45 m in Figure 26 is probably more a reflection of incomplete collecting at that depth rather than any real minimum value). Like *Hydrolithon breviclavium*, *L. pallescens* is generally replaced by melobesioid species on the abundant small nodules occurring below depths of 80 m. Littler (1973b) describes in detail the occurrence of rhodolith communities off the island of Oahu at depths of 8–28 m; however, that author did not differentiate between the sympatric *L. pallescens* and *H. breviclavium* occurring in this study site.

A morphological and ecological "pair species" of this plant has not been found in the Caribbean.

Lithophyllum ganeopsis, new species

FIGURES 23, 28

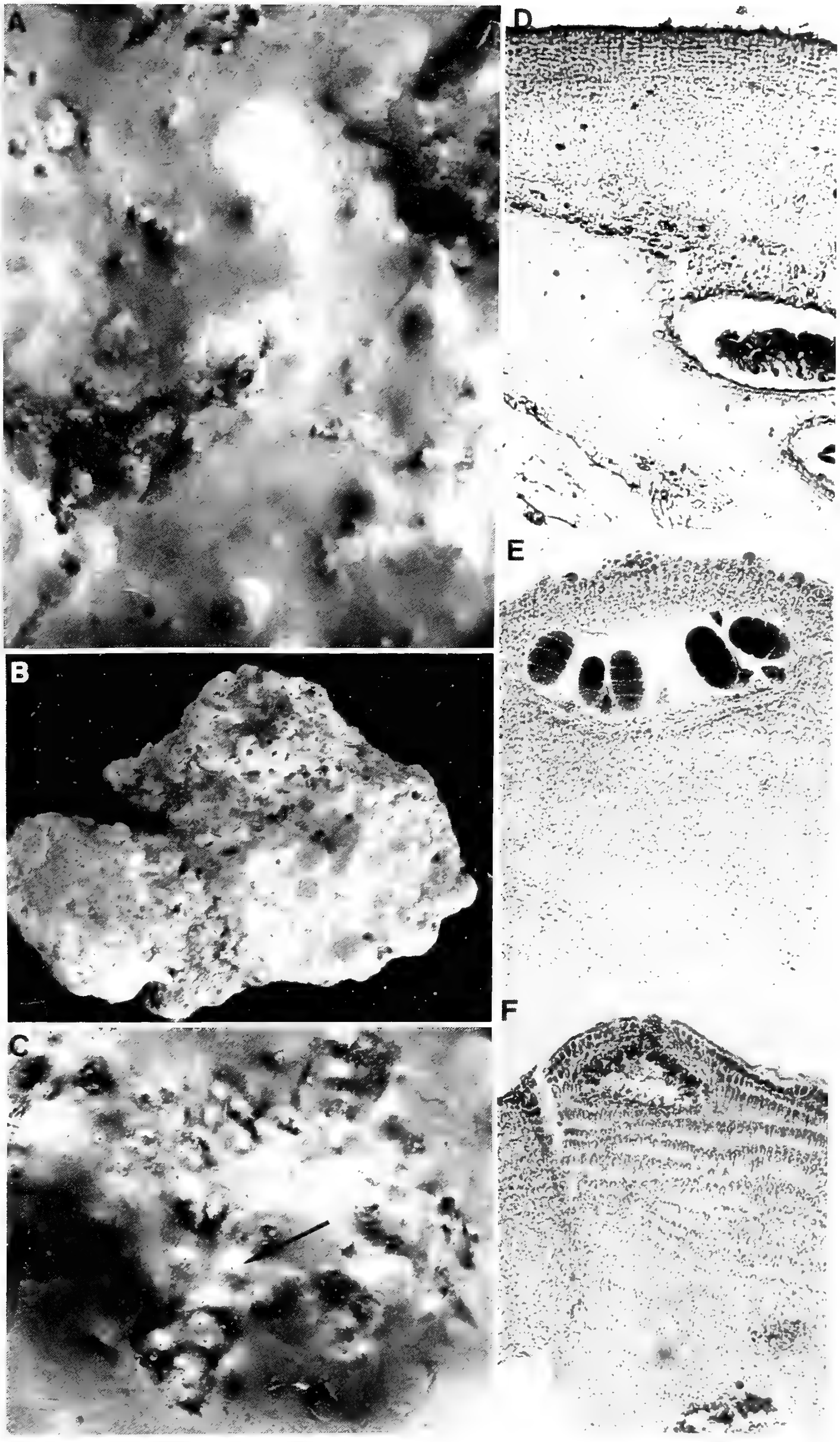
DESCRIPTION.—Crustae bene evolutae usque aliquot mm crassitudine, superficie maxime nitida (Figura 28A,B); conceptacula non perspicua, paululum elevata fortuite sparsa (Figura 28C). Epithallium unistratosum, raro duostratosum; 2–5 μm long. atque 6–9 μm diam. Meristema intercalare relative breve, cellulis 6–11 μm long. et 5–8 μm diam. Perithallium pluristratosum, saepe regulariter stratosum (Figura 28D), foveo-colligationes secondariae abundates; cellulis 4–16 μm long. et 4–12 μm diam. (Figura 23). Hypothallium ex unico strato cellularum plerumque isodiametricarum (7–19 μm long., 7–14 μm diam.) constans. Conceptacula tetrasporangialia uniporata, paululum elevata (Figura 28C,E), 250–500 μm O.D., 140–300 μm I.D. atque 60–120 μm alt., in perithallio obruta; tetrasporangia per pavimentum conceptaculi disposita, 40–65 μm long., 20–40 μm diam. Conceptacula procarpica non visa. Conceptacula cystocarpica uniporata, elevata (100 μm), 230–280 μm I.D., 70–80 μm alt., carposporangia ad periferiam conceptaculi restricta; cellula-coalescens discoidea, 150–200 μm diam.; carposporae 50 μm long.; 25 μm diam. Conceptacula mascula uniporata, elevata (60 μm), 230–310 μm I.D., 40–60 μm alt.; cellulae-matricales 2 extensiones spermatiales habente; spermatia discoidea ad ellipsoidea, 3–4 μm long., 2–3 μm diam. intra fila mucosa reperta (Figura 28F).

Well-developed crusts reaching a thickness of several mm, surface highly glossy (Figure 28A,B); indistinct, slightly raised, randomly scattered conceptacles (Figure 28C). Epithallium single (rarely 2) cell layers; cells 2–5 μm long and 6–9 μm diam. Intercalary meristem relatively short; cells 6–11 μm long and 5–8 μm diam. Perithallium multilayered, often regularly layered (Figure 28D), abundant secondary pit connections; cells 4–16 μm long and 4–12 diam. (Figure 23). Hypothallium a single layer of generally isodiametric cells (7–19 μm long, 7–14 μm diam.). Tetrasporangial conceptacles unipored, raised slightly (Figure 28C, E), 250–500 μm O.D., 140–300 μm I.D. and 60–120 μm high, buried in perithallium; tetrasporangia across floor of conceptacle, 40–65 μm long, 20–40 μm diam. No procarpic conceptacles seen. Cystocarpic conceptacles uniporate, raised (100 μm), 230–280 μm I.D., 70–80 μm high; carposporangia restricted to periphery of conceptacle; fusion cell discoid, 150–200 μm diam.; carpospores 50 μm long, 25 μm diam. Male conceptacles uniporate raised (60 μm), 230–310 μm I.D., 40–60 μm high; spermatangial mother cells restricted to the conceptacle floor, 2 spermatial extensions per mother cell; spermatia discoid to ellipsoidal, 3–4 μm long, 2–3 μm diam., within mucus strands (Figure 28F).

TYPE-LOCALITY.—Honauma Bay, Oahu, Hawaii (21°15′N, 157°20′W); windward, 8 m.

HOLOTYPE.—D. Child 71-53-23, March 1971 (USNC), Figure 28A,B.

FIGURE 28.—*Lithophyllum ganeopsis*, new species: A, surface of type specimen, × 10; B, habit of type specimen, × 1; C, surface view with conceptacles (arrowed), × 10; D, section through vegetative thallus, note single-layered hypothallium (arrowed), × 150; E, tetrasporangial conceptacle, × 150; F, male conceptacle, note spermatia in strands along roof of conceptacle, × 150. (Specimen nos.: A, B, 71-53-23; C, D, 71-56-5; E, 71-81-6; F, 71-81-29.)


A
B
C
D
E
F

PARATYPES.—*Hawaii:* Honaunau, March 1971, 71-56-5; Kaneohe, August 1971, 71-81-6, 71-81-29. *Necker:* August 1971, 71-76-1.

REMARKS.—The specific epithet *ganeopsis* refers to the glossy surface common to this species.

Tetrasporangial and cystocarpic conceptacles are buried in the perithallium with both tetrasporangial and carposporangial remains within the conceptacle cavity. Overgrowth occurs from the roof of the conceptacle.

Lithophyllum ganeopsis is a very distinctive but infrequent plant in our collections. Its maximum abundance for any one zone was 2% of the collected specimens. Although most of the plants found occurred from the intertidal to 10 m depth, a few were taken at depths of 30 m. We do not know of a Caribbean "pair species," though *Lithophyllum nitorum* that W. and P. Adey described for the temperate eastern Atlantic (Adey and Adey, 1973) is morphologically similar.

Lithophyllum insipidum, new species

FIGURES 23, 29

DESCRIPTION.—Crustae non amplae, satis crassae, autem, factae (usque ad 1 cm) rosaceae ad lavandulas, saepe maculas albas non perspicuas praebentes, superficie tessellata distincte sed irregulariter plerumque facta (Figura 29B,C,F). Conceptacula plerumque abundantia, parva, paululum elevata (Figura 29F). Epithallium ex unico strato cellularum (3–6 μm long., 6–10 μm diam.) constans (Figura 29D). Meristema intercalare perspicuum, elongatum, cellulis 11–20 long. atque 6–9 μm diam. (Figura 29D). Perithallium pluristratosum, foveo-colligationes secondarias abundantes praebens (Figura 29D), bene stratosum, cellulis 4–22 μm long. atque 5–10 μm diam. (Figura 23). Hypothallium unistratosum (Figura 29A); cellulis 12–16 μm long. atque 12–19 μm diam. Conceptacula tetrasporangialia uniporata, paululum elevata (30–70 μm), 450–750 μm O.D., 170–230 μm I.D., 80–140 μm alt. (Figura 29A); tetrasporangia ad periferiam conceptaculi restricta, columella adest, 40–100 μm long., 20–50 μm diam.

Crusts not extensive but becoming quite thick (to 1 cm), pink to lavender, often with indistinct white patches, surface usually becoming distinctly though irregularly tessellate (Figure 29B, C,F); conceptacles usually abundant, small, slightly raised (Figure 29F). Epithallium a single layer of cells (3–6 μm long, 6–10 μm diam.) (Figure 29D). Intercalary meristem distinct, elongate; cells 11–20 μm long and 6–9 μm diam. (Figure 29D). Perithallium, multilayered, with abundant secondary pit connections (Figure 29D), well layered; cells 4–22 μm long and 5–10 μm diam. (Figure 23). Hypothallium a single cell layer (Figure 29A); cells 12–16 μm long and 12–19 μm diam. Tetrasporangial conceptacles unipored, slightly raised (30–70 μm), 450–750 μm O.D., 170–230 μm I.D., 80–140 μm high (Figure 29C); tetrasporangia restricted to the conceptacle periphery, columella present, 40–100 μm long, 20–50 μm diam. Sexual plants not found.

TYPE-LOCALITY.—Waikiki, Oahu, Hawaii (21°10′N, 157°55′W), leeward, 3–5 m depth.

HOLOTYPE.—D. Child, 71-50-17, March 1971 (USNC), Figure 29B.

PARATYPES.—*Hawaii:* Hilo, March 1971, 71-58-39; Honaunau, March 1971, 71-55-71. *Midway:* South Island, August 1971, 71-82-32. *Oahu:* Waianae, March 1971, 71-52-25; Waikiki, March 1971, 71-50-17.

DISTRIBUTION.—Southern part of archipelago.

REMARKS.—Specific epithet refers to the "dull" patchy appearance of this species in contrast to the typical glossy *Lithophyllum* surface.

Although the anatomy of this plant is typically that of the genus *Lithophyllum*, and thus strikingly different from *Hydrolithon*, *L. insipidium*, with its lavender color and tessellate surface, may be confused with *Hydrolithon reinboldii*. Thicker plants with the color and texture of *H. reinboldii* that are lacking mammillons or with relatively small conceptacles should be investigated closely to determine whether they are *H. reinboldii* or *L. insipidum*. Examination of a fractured vertical surface for the irregular, almost porous perithallium (due to extensive fusions) or *H. reinboldii* should easily

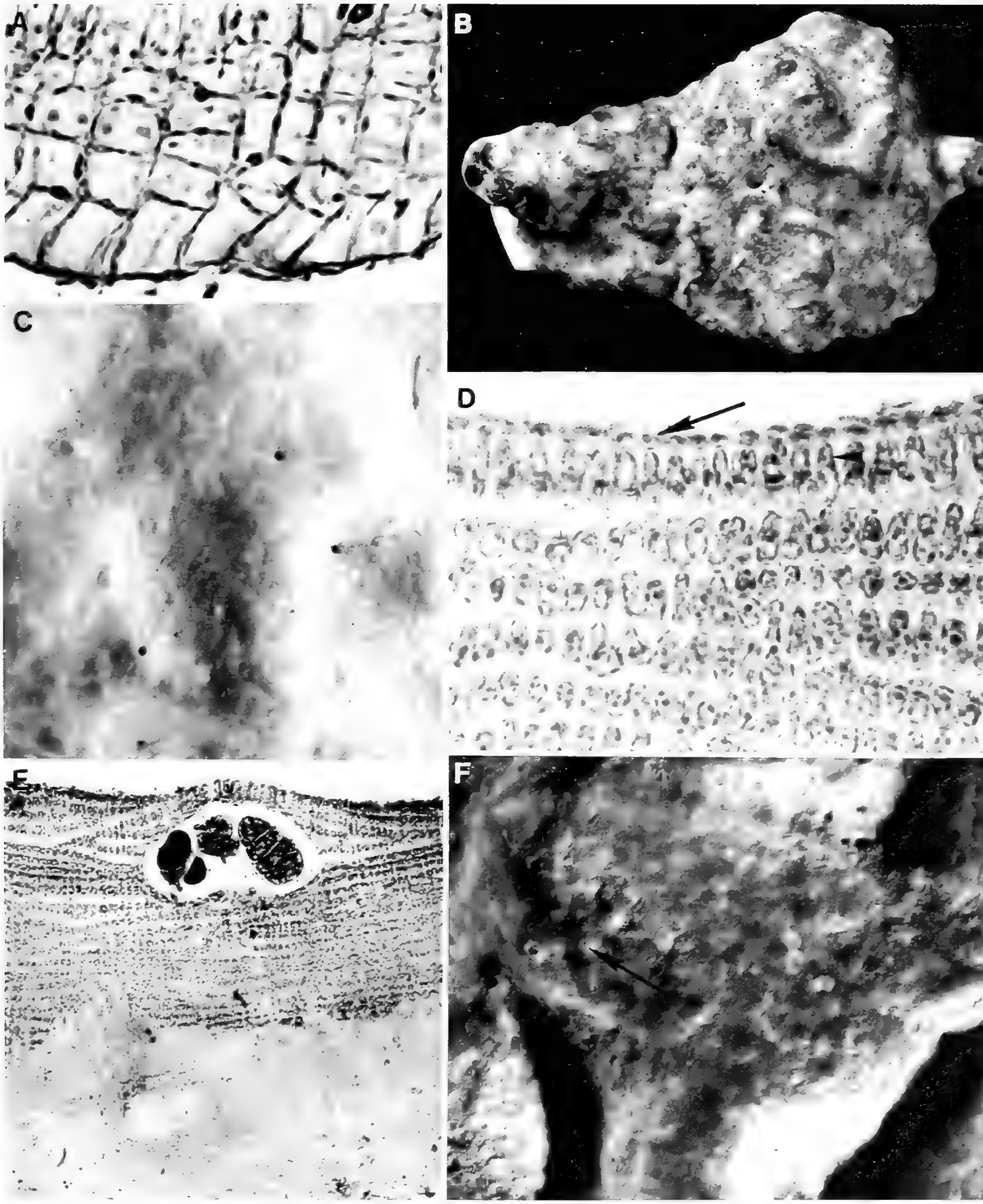


FIGURE 29.—*Lithophyllum insipidum*, new species: A, section through thallus showing lower vegetative tissue, × 600; B, habit of type specimen, × 1; C, surface of type specimen showing tesselate pattern, × 10; D, section through thallus epithallium (arrowed), intercalary meristem (arrowhead), and perithallium, × 300; E, tetrasporangial thallus, note conceptacle and region of new growth, × 150; F, surface of type specimen with conceptacles (arrow), × 10. (Specimen nos.: A, 71-52-25; B, C, F, 71-50-17; D, 71-82-32; E, 71-58-39; micrographs reduced to 93%.)

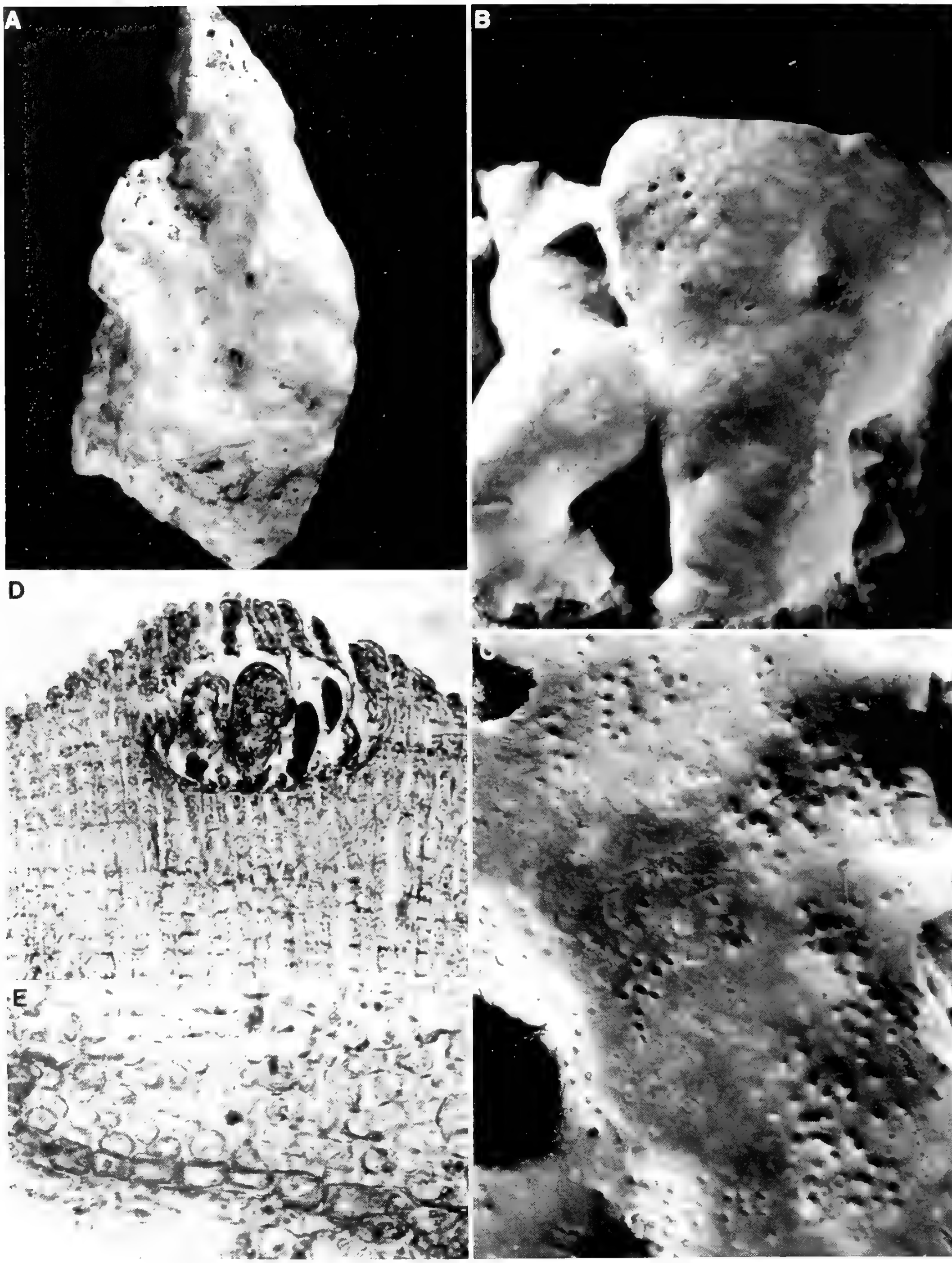


FIGURE 30.—*Lithophyllum punctatum:* A, habit, × 1; B, surface with intact conceptacles, × 10; C, surface with spent conceptacles, × 10; D, tetrasporangial conceptacle, × 250; E, section of vegetative tissue showing hypothallium, × 300. (Specimen nos.: A, 71-52-20; B, 71-54-8; C, 71-52-30; D, 71-53-32; E, 71-50-7; micrographs reduced to 83%.)

differentiate a crust from the even, fine-grained, and layered *Lithophyllum* pattern.

Lithophyllum insipidum was more abundant in our collections than *L. ganeopsis*, but still is only occasional, reaching a maximum zonal abundance of 6% from 0 to 3 m. A few specimens were found from 15 to 35 m, but most occurred from low water to 10 m.

Lithophyllum punctatum Foslie

FIGURES 23, 30

Lithophyllum punctatum Foslie, 1906:22.

DESCRIPTION.—Surface dull and appearing dry, pink-lavender color, crusts becoming fairly thick, to several mm (Figure 30A,B); conceptacles generally abundant, level with surface or slightly raised, scattered randomly over the surface, leaving open pits after spore release (Figure 30B,C). Epithallium 1 to 3 cell layers; cells 2–6 μm long and 6–12 μm diam. Intercalary meristem of randomly elongating cells (5–9 μm long, 6–8 μm diam.). Perithallium multilayered, secondary pit connections present, scattered large cells at surface (16–18 μm long, 10–11 μm diam.), adjacent cells varying in size and position, tissue appearing as a system of loose independent vertical strands; cells elongating greatly with depth in the tissue (3–13 μm long, 4–10 μm diam.) (Figure 23). Hypothallium a single cell layer; cells isodiametric to horizontally elongate, 7–16 μm long and 6–10 μm diam. (Figure 30E). Tetrasporangial conceptacles unipored, raised 40–50 μm above the surrounding crust, 160–170 μm I.D., 60–70 μm high (Figure 30D); tetrasporangia restricted to periphery of conceptacle, columella present, 40–80 μm long and 20–65 μm diam. No sexual material collected.

TYPE-LOCALITY.—Tricomalie, Ceylon.

HOLOTYPE.—Svedelius, 17 April 1903, in herbarium of M. Foslie (TRH). Isotype: USNC.

DISTRIBUTION.—Ceylon, the island of Oahu.

SPECIMENS STUDIED.—*Oahu:* Honauma, March 1971, 71-53-32; Kaneohe, March 1971, 71-54-8; Waianae, March 1971, 71-52-20, 71-52-30; Waikiki, March 1971, 71-50-7.

REMARKS.—We found only 10 specimens of this species, all from less than 10 m depth. Recently, a similar plant as yet undescribed (Adey, unpublished data) was found in the Caribbean, on the shallow algal pavements of Martinique.

MELOBESIOIDEAE (J.E. Areschoug) Yendo, 1902

Archaeolithothamnium Rothpletz, 1891

The authors realize that the use of *Archaeolithothamnium* over *Sporolithon* Heydrich (1897b) has been questioned (Papenfuss, 1968). In this paper, we shall use *Archaeolithothamnium.*

There has been considerable concern in recent years over the taxonomic position of this genus. Adey (1970; Adey and Johansen, 1972) placed *Archaeolithothamnium* in the subfamily Melobesioideae, closely related to *Lithothamnium.* Cabioch (1972), because of the apparent presence of secondary pits, has placed the genus in a separate subfamily, the Sporolithoideae Setchell (1943: 134). Womersley (pers. comm.), on the other hand, has suggested that, because of the occasional presence of cruciate tetrasporangia, perhaps the genus should be placed in a separate new family.

Our position remains unchanged in this regard. Even though transmission electron microscope studies of Australian members of *Archaeolithothamnium* (as *Sporolithon*, Townsend, unpublished data) have shown the presence of secondary pit connections as well as lateral cell fusions, the cover cells or epithallial cells and the meristem cells of both *Lithothamnium* and *Archaeolithothamnium* are quite similar (Adey and Macintyre, 1973). This type of cover cell is unique in the Corallinaceae and other Melobesioideae. In addition, the sporangial caps that define the subfamily Melobesioideae are present in *Archaeolithothamnium*, though they are generally smaller than in other genera. While it is true that the sporangia sometimes develop cruciately, this is unusual, the zonate development being more typ-

ical in Hawaiian species of *Archaeolithothamnium*. It is our opinion that the nature of the epithallium and the presence of sporangial caps far outweigh these irregularities in indicating the relationship of the genus. We feel that *Lithothamnium* is very closely related to *Archaeolithothamnium*, probably having evolved from it during the mid to late Mesozoic (Adey and Macintyre, 1973).

Key to the Species of *Archaeolithothamnium*

Glossy, red-brown crusts, sometimes mammillate or with short branches, with generally extensive sori (> 5 mm diam.) and narrow sporangial pores (not visible with a hand lens or barely so) .... ***A. erythraeum***

Glossy, red to pink crusts, sometimes having small irregular branches, with small sori (< 5 mm diam.) bearing large sporangial pores (easily visible with a hand lens). .... ***A. episoredion,*** new species

Archaeolithothamnium erythraeum (Rothpletz) Foslie

FIGURES 31–33

Archaeolithothamnium erythraeum (Rothpletz) Foslie in Weber-van Bosse and Foslie, 1904:39.—Foslie, 1900c [nomen nudum]; 1907a; 1908a.—Littler, 1971b; 1973a.—Setchell, 1924; 1926.

Lithothamnium erythraeum Rothpletz, 1893:5.

Sporolithon erythraeum (Rothpletz) Kylin, 1956:205.—Papenfuss, 1968.—Womersley and Bailey, 1970.

DESCRIPTION.—Crusts thick, often growing nonadherent to substrate sometimes developing mammillons, surface smooth, glossy (Figure 31A) bright bluish red to brown. Cover cells "*Lithothamnium*-type" (Figure 31C,D) forming a single layer over the epithallium; cells 2–7 μm long and 5–10 μm diam. Intercalary meristematic cells 5–8 μm long and 5–11 μm diam. Perithallium multilayered regular, lateral cell fusions and secondary pit connections present (Figure 31B); cells square, tending to elongate and enlarge with depth in tissue (Figure 32), 5–12 μm long and 4–15 μm diam. Hypothallium multilayered, parallel to weakly coaxial, 30–110 μm thick; cells 13–34 μm long and 6–9 μm diam. Tetrasporangial sori buried in tissue (Figure 31E), surface sori not seen in collections; tetrasporangia 60–90 μm long and 25–40 μm diam.

TYPE-LOCALITY.—Red Sea.

HOLOTYPE.—Unknown (Papenfuss, 1968; possibly destroyed in Berlin bombings).

DISTRIBUTION.—Borneo, Celebes, Hawaii, Indian Ocean, New Guinea, Philippines, Red Sea, Samoa, Solomon Islands, Tahiti, Timor.

SPECIMENS STUDIED.—*Midway:* lagoon, March 1971, 71-62-8; South Island, August 1971, 71-82-63, 71-82-69. *Oahu:* Honauma, March 1971, 71-53-24; Waikiki, March 1971, 71-50-61.

REMARKS.—*Archaeolithothamnium erythraeum* is not an abundant plant in our collections. In contrast to the abundant deep-water *Archaeolithothamnium episoredion*, new species, most of the *A. erythraeum* were taken between low water and 15 m (Figure 33). Doty (1974, as *Sporolithon*) indicated that an *Archaeolithothamnium* species is a major sublittoral shade element of Pacific algal ridges, but he did not recognize the numerous *Neogoniolithon* species that tend to dominate such environments in both the Caribbean and Hawaii. We suggest that Doty's *Hydrolithon* and *Sporolithon* "communities" may include, or even be dominated by, *Neogoniolithon* species.

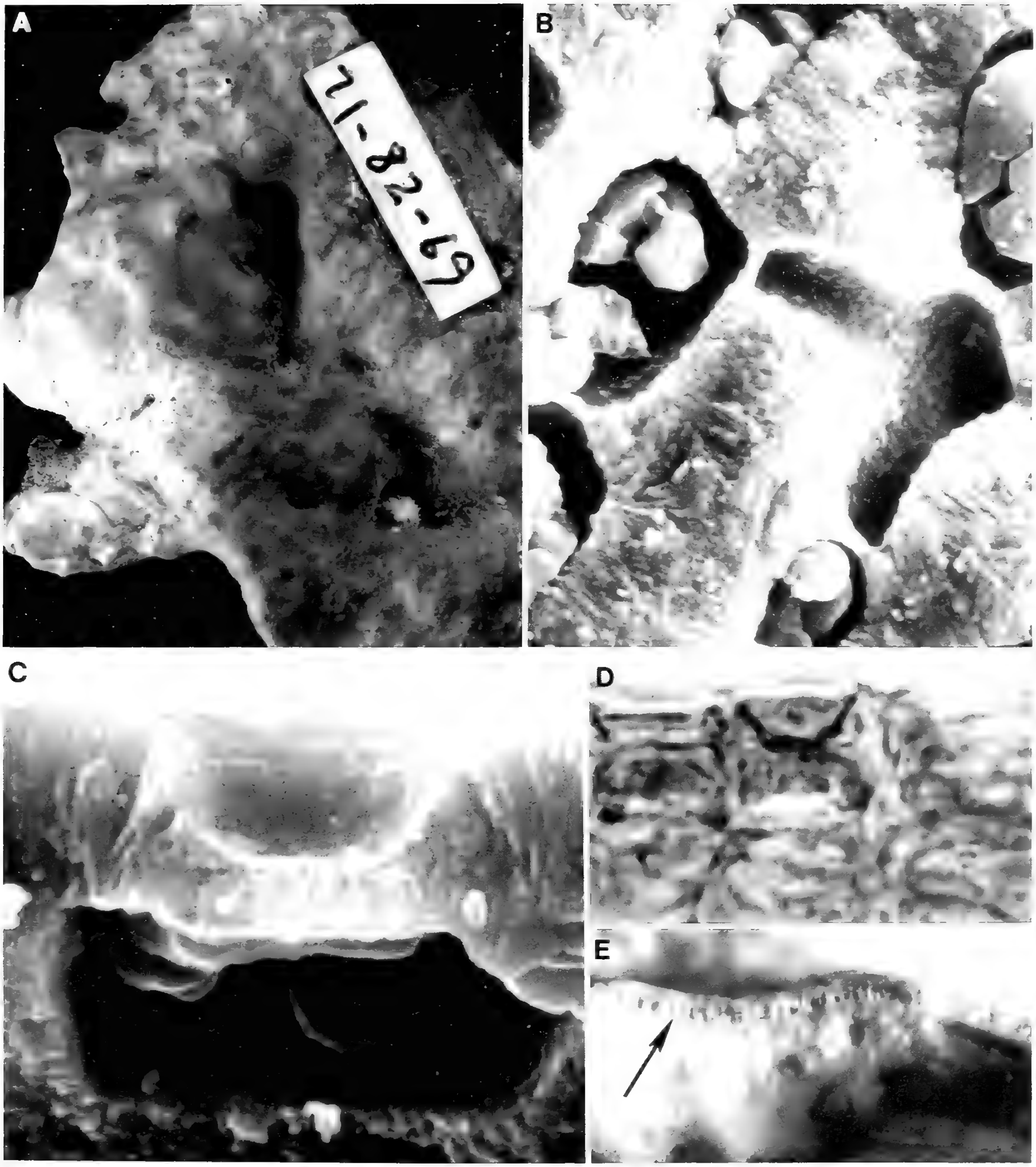


FIGURE 31.—*Archaeolithothamnium erythraeum:* A, habit of typical specimen, × 2; B, scanning electron micrograph of perithallium in area of secondary pit connection; × 2500; C, scanning electron micrograph of "*Lithothamnium*-type" cover cell, × 7500; D, light micrograph of "*Lithothamnium*-type" cover cell, × 2000; E, thallus with buried sorus (arrow), × 20. (Specimen nos.: A, 71-82-69; B, C, 71-53-24; D, E, 71-82-63; micrographs reduced to 95%.)

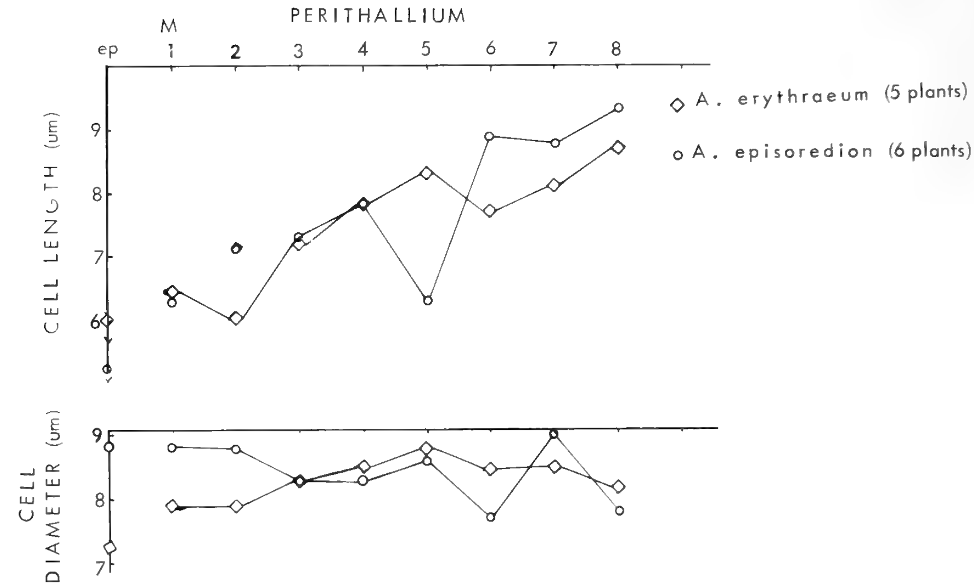


FIGURE 32.—Mean epithallial and perithallial cell dimensions of *Archaeolithothamnium erythraeum* and *A. episoredion*, new species.

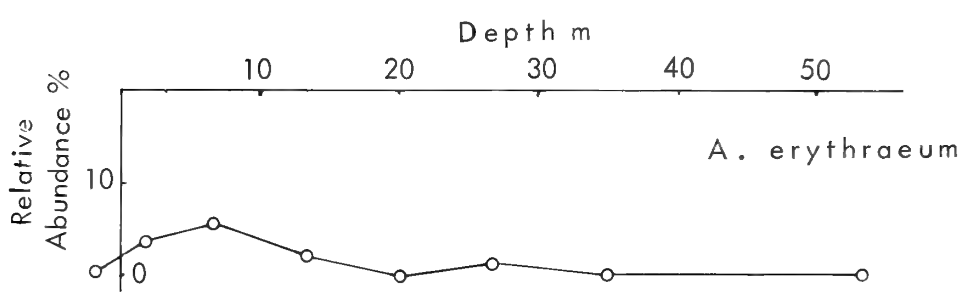


FIGURE 33.—Depth distribution of *Archaeolithothamnium erythraeum*.

Archaeolithothamnium erythraeum is the "pair species" of the Caribbean alga *Archaeolithothamnium dimotum*, which appears very similar in habit and anatomy. *Archaeolithothamnium dimotum* occurs in shallow areas, favoring strongly shaded situations (in holes around the bases of coral heads or under *Sargassum*) on reef flats. We have not seen a mammillate form of *A. dimotum*; however, the relationship between the crustose and mammillate forms of *A. erythraeum* is not entirely clear at present. These plants are relatively minor elements in both our Caribbean and Hawaiian collections and are in need of considerable additional study.

Archaeolithothamnium episoredion, new species

FIGURES 32, 34, 35

DESCRIPTION.—Crustae leves nitidae (Figura 35A) dilute rosaceae ad laete rubiginosus, amplae factae; sori elevati, ovales usque ad aliquot mm dimensione longissima, poris obturaculisve sporangialibus magnis, facile visibilibus (oculo armato) praediti (Figura 35B,C). Cellulae obtegentes typi *Lithothamnii* (Figura 35E), 2–4 µm long. atque 2-7 µm diam. cellulae meristematis intercalaris 4–8 µm long. atque 6–10 µm diam. Perithallium regulare, pluristratosum, cellulis quadratis, progredienter longioribus profundioribus in tela (Figura 32), 4–18 µm long. atque 5–13 µm diam. Hypothallium pluristratosum, parallelum, 20–60 µm crass.; cellulis 4–25 µm long. et 5–10 µm diam. Sori superficiales, in perithallio interdum obruti (Figura 35D), post liberationem sporangialem flaviformes facti (Figura 35B,C); tetrasporangia zonata, 70–200 µm long. atque 35–100 µm diam.

Smooth, glossy crusts (Figure 35A) light pink to bright brownish red, becoming extensive; raised oval sori reaching several mm in longest dimension with large, easily visible (with a hand lens) sporangial pores or plugs (Figure 35B,C). Cover cells "*Lithothamnium*-type" (Figure 35E), 2–4 µm long and 2–7 µm diam. Intercalary meristem cells 4–8 µm long and 6–10 µm diam. Perithallium regular, multilayered; cells square, becoming increasingly elongate with depth (Figure 32), 4–18 µm long and 5–13 µm diam. Hypothallium multilayered, parallel, 20–60 µm thick; cells 14–25 µm long and 5–10 µm diam. Sori superficial, sometimes buried in perithallium (Figure 35D), upon sporangial release becoming "honeycomb"-like (Figure 35B,C); tetrasporangia zonata, 70–200 µm long and 35–110 µm diam. Sexual thalli were not seen.

TYPE-LOCALITY.—St. Rogatien Bank, northwest, Hawaii (24°15′N, 167°0′W), 70–95 m.

HOLOTYPE.—D. Child, 71-79-(35-47f), August 1971 (USNC), Figure 35A.

PARATYPES.—*Hawaii:* Honaunau, March 1971, 71-55-18. *Maui:* south-central coast, August 1971, 71-67-9. *Nihoa:* west coast, August 1971, 71-75-4. *Oahu:* Waikiki, March 1971, 71-50-77.

DISTRIBUTION.—South and central archipelago.

REMARKS.—The specific epithet *episoredion* refers to the superficial nature of the sori.

This species is abundant in deep water and is an important builder of rhodoliths (Figure 34). It is very similar to the Caribbean *Archaeolithothamnium episporum* Howe (1918a), which was described from shallow water and we have consistently found in deep water elsewhere in the Caribbean (Adey, unpublished data). We have artificially kept the species separate, even though it has meant the perhaps unnecessary description of a new taxon. In the tropical East Pacific, two species with similarly small sori have been described (*A. howei* Lemoine; *A. pacificum* Dawson), but both of these generally have smaller cells and sporangia.

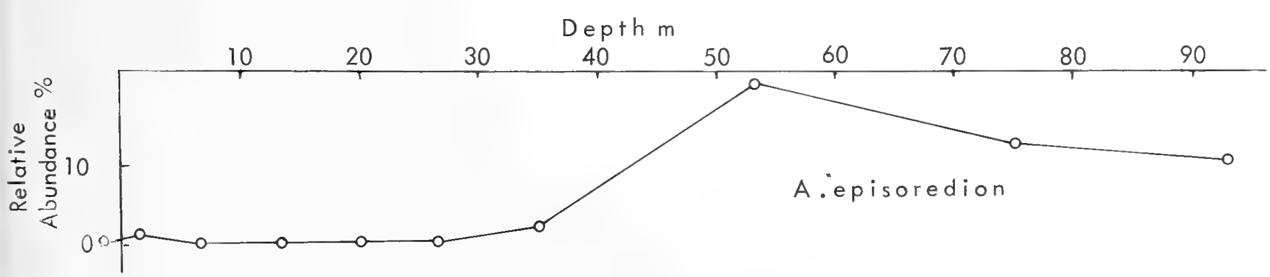


FIGURE 34.—Depth distribution of *Archaeolithothamnium episoredion*, new species.

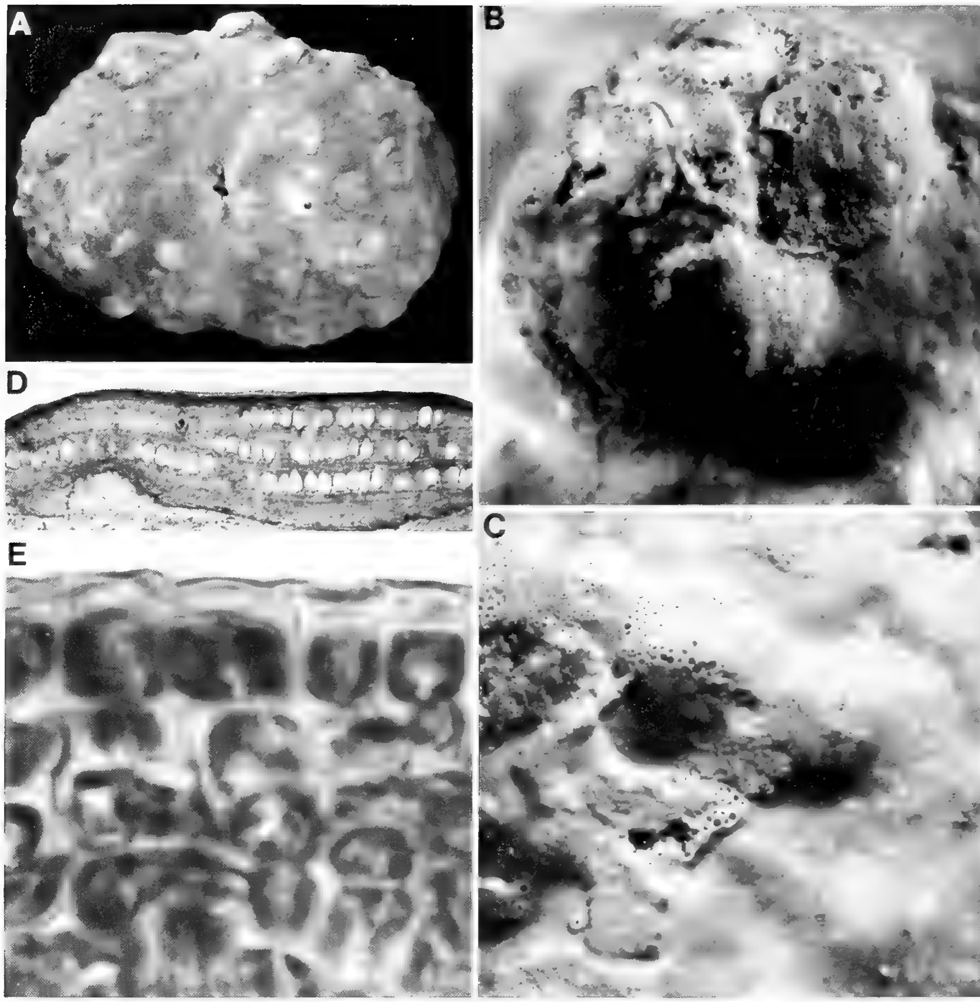


FIGURE 35.—*Archaeolithothamnium episoredion*, new species: A, habit of type specimen, × 2; B, C, surface of thallus showing sori, note large sporangial pores, × 10; D, section through thallus showing buried sori, × 20; E, section through thallus showing cover cells, × 1500. (Specimen nos.: A, 71–79–(35–47f); B, C, 71-67-9; D, E, 71-55-18.)

We collected two small rhodolith specimens of *Archaeolithothamnium* from 70–90 m, one with an almost smooth surface, the other with abundant short branches (1–2 mm long) about 1 mm diam. Both of these plants had sori that were only 400–600 μm in outside diam., smaller than the conceptacles of many species of *Lithothamnium* (see below, *L. pulchrum* Weber-van Bosse & Foslie in Foslie); however, these small sori showed the basal "honeycomb" pattern indicating partial calcification between the individual sporangia characteristic of *Archeolithothamnium.* In section, narrow fusions or apparent secondary pits are present, along with the larger cell fusions, and the sporangial cap walls are very short. These specimens have been tentatively placed with the anatomically similar *A. episoredion*, though it may be that they belong to a separate species. In this case, it is interesting to note that the difference between an *Archaeolithothamnium* sorus and a *Lithothamnium* conceptacle is not marked, even though this characteristic has been used for generic, subfamily, and even family differentiation in crustose corallines.

Lithothamnium Philippi, 1837

Key to the Species

Extensive leafy pink-brown crusts becoming nodular and eventually developing coarse branches (branches 2–5 mm diam.); large conceptacles > 500 μm, O.D. .... ***L. pulchrum***

Thin, bright-red crusts developing abundant, narrow often irregular branches, 0.5-2 mm diam.; conceptacles < 500 μm, O.D. .... ***L. australe***

Lithothamnium pulchrum Weber-van Bosse & Foslie

FIGURES 36–38

Lithothamnium pulchrum Weber-van Bosse & Foslie in Foslie, 1902a:3.—Weber-van Bosse and Foslie, 1904.

Mesophyllum pulchrum (Weber-van Bosse & Foslie in Foslie) Lemoine, 1928:252.

DESCRIPTION.—Rather leafy, medium thin plants (200–500 μm thick) with large raised multipored conceptacles; developing numerous knobs and eventually large irregular branches 2–5 mm diam. (Figure 36A,B). Cover cells "*Lithothamnium*-type," single cell layer; cells 1–4 μm long and 3–10 μm diam. Intercalary meristem medium length; cells 3–6 μm long and 5–10 μm diam. Perithallium multilayered, abundant fusions, scattered staining bodies (phosphotungstic haematoxylin) (Figure 36c); cells 3–9 μm long and 9–22 μm diam. (Figure 37). Hypothallium multilayered, noncoaxial, 20–65 μm thick; cells 3–11 μm long and 4–11 μm diam. (Figure 36c). Tetrasporangial conceptacles multipored, strongly raised (Figure 36E) 500–1000 μm O.D., 360–470 μm I.D., 170–250 μm high; tetrasporangia not seen. Sexual conceptacles seen, but not sectioned (Figure 36D).

TYPE-LOCALITY.—Sailus Besar, Paternoster Islands, Indonesia (station 315, *Siboga* Expedition), 36 m depth.

HOLOTYPE.—Weber-van Bosse, 19–21 February 1900, in herbarium of M. Foslie (TRH). Isotype: USNC.

DISTRIBUTION.—Celebes.

SPECIMENS STUDIED.—*Hawaii:* Honaunau, March 1971, 71-55-25. *Maui:* south-central, August 1971, 71-67-1, 71-68-14. *Midway:* South Island, August 1971, 71-82-29. *Oahu:* Waikiki, March 1971, 71-50-128. *St. Rogatien Bank:* August 1971, 71-79-9, 71-79-11.

REMARKS.—Next to *Lithothamnium australe* Foslie in Weber-van Bosse & Foslie, *L. pulchrum* was the most abundant species encountered at depths greater than 60 m (Figure 38). Scattered plants were taken in shallow water, and whereas no data on microhabitat were recorded, judging by the habit of *Lithothamnium* on algal ridges and coral reefs in the Caribbean, these were probably from cryptic locations. *Lithothamnium pulchrum* is a major rhodolith former on the Hawaiian banks and was especially abundant on St. Rogatien Bank.

Lithothamnium australe Foslie

FIGURES 37, 39, 40

Lithothamnium australe Foslie in Weber-van Bosse & Foslie, 1904:24.—Foslie, 1907a.—Dawson, 1944; 1954a; 1960b. —Taylor, 1945.

Lithothamnium australe Foslie, 1900c:13 [nomen nudum].

Lithothamnium corallioides P. & H. Crouan f. *australis* Foslie, 1895:8.

Lithothamnium australe Foslie f. *americana* Foslie in Weber-van Bosse and Foslie, 1904:25.

Lithophyllum australe (Foslie) Lemoine, 1917:131.

Mesophyllum australe (Foslie) Lemoine, 1928:252; 1929.

DESCRIPTION.—Light pink to bright red plants, usually with sparse primary branches (2–6 mm diam.) bearing numerous small, very irregular projections 0.5-2 mm diam. (Figure 39A,D,E); conceptacles medium-sized, rather rounded, flat-

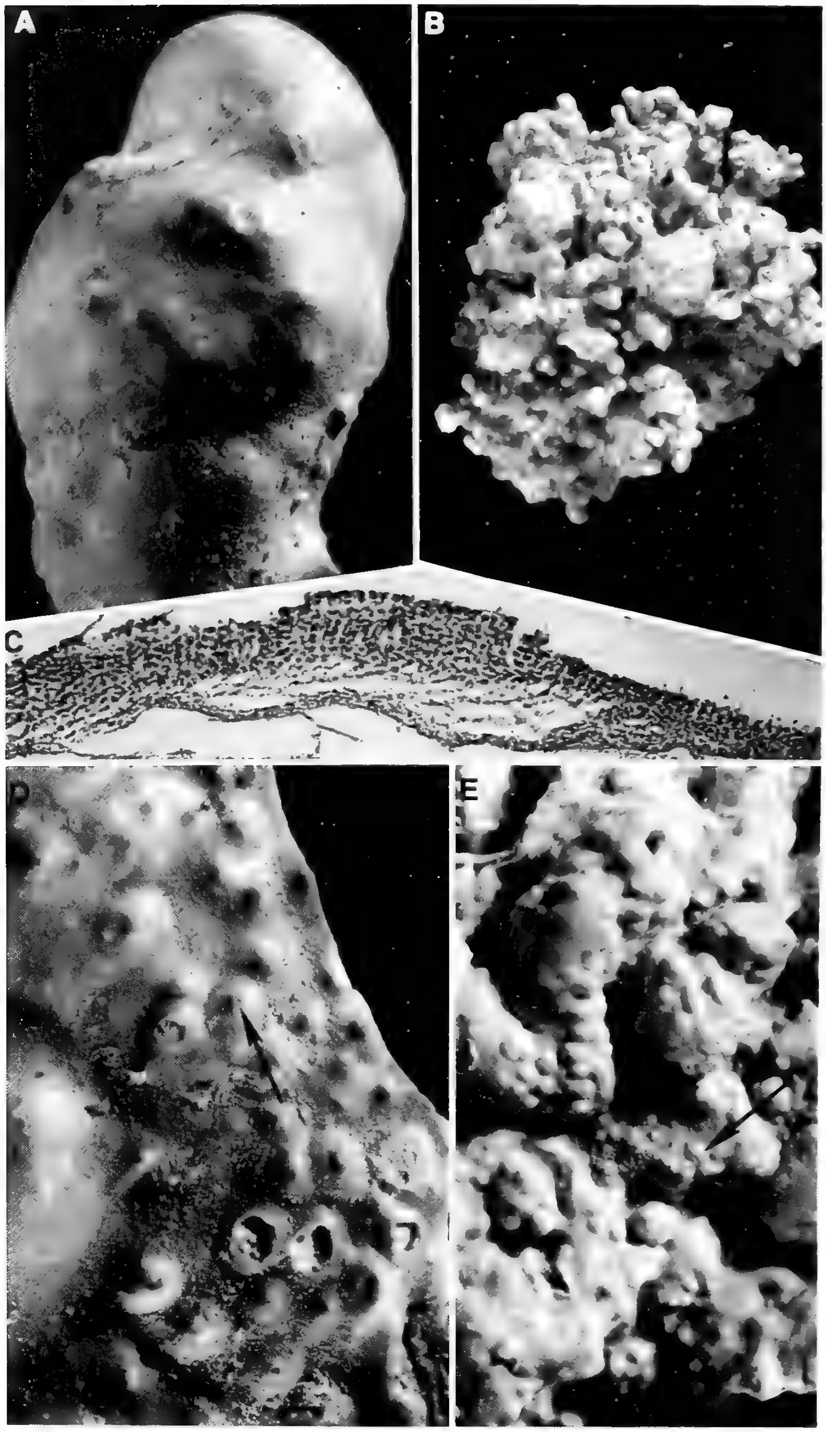


FIGURE 36.—*Lithothamnium pulchrum:* A, branch of thallus, × 20; B, habit, × 1; C, section through vegetative crust, × 150; D, sexual crust with conceptacles (arrow), × 10; E, tetrasporangial conceptacles (arrow), × 5. (Specimen nos.: A, B, 71–79–9; C, 71–79–11; D, 71-68-14; E, 71-67-1; micrographs reduced to 94%.)

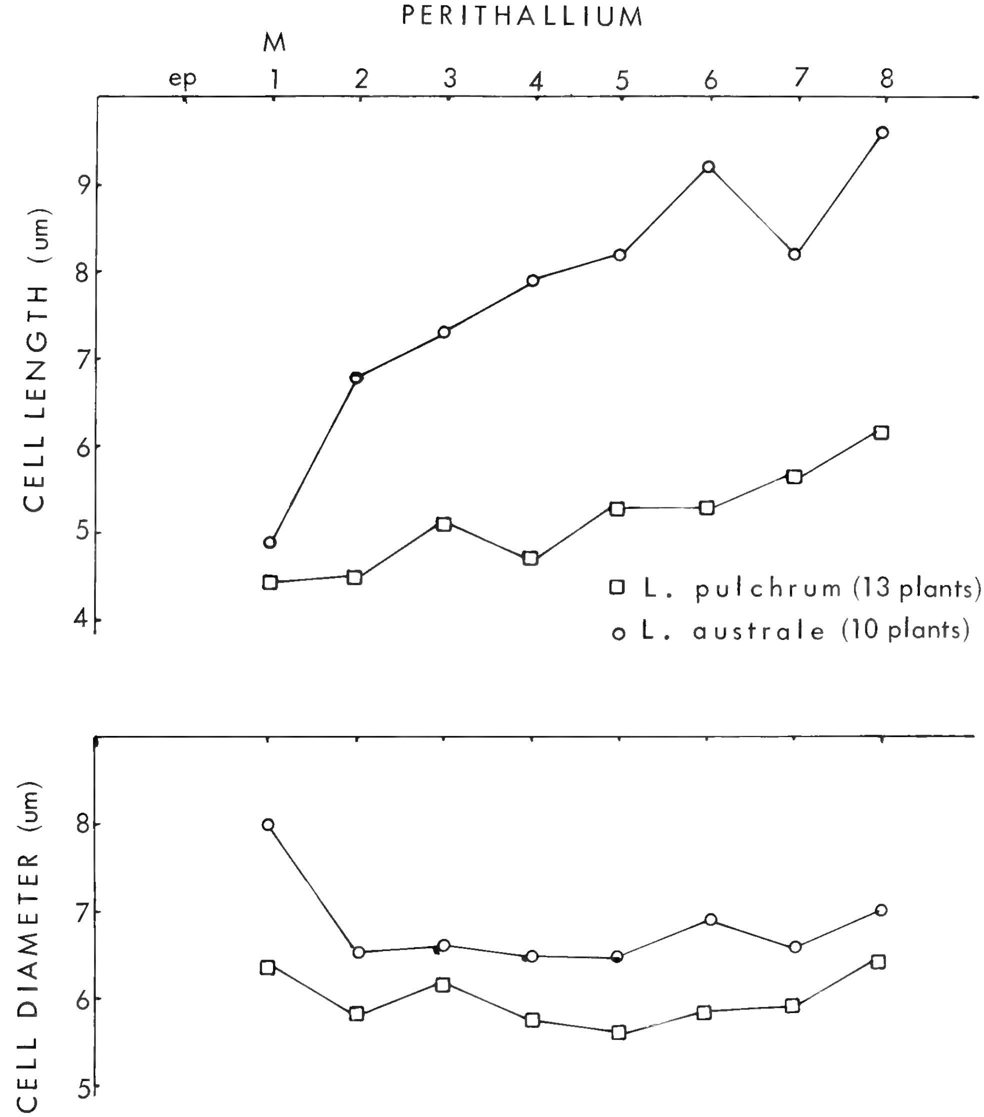


FIGURE 37.—Perithallial cell dimensions of *Lithothamnium pulchrum* and *L. australe*.

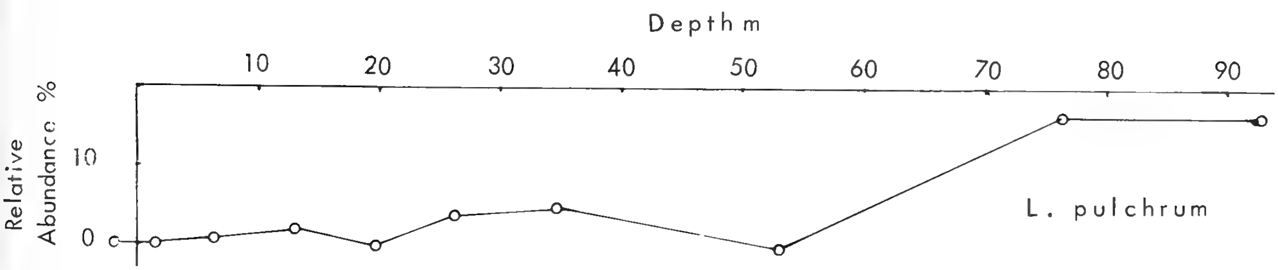


FIGURE 38.—Depth distribution of *Lithothamnium pulchrum*.

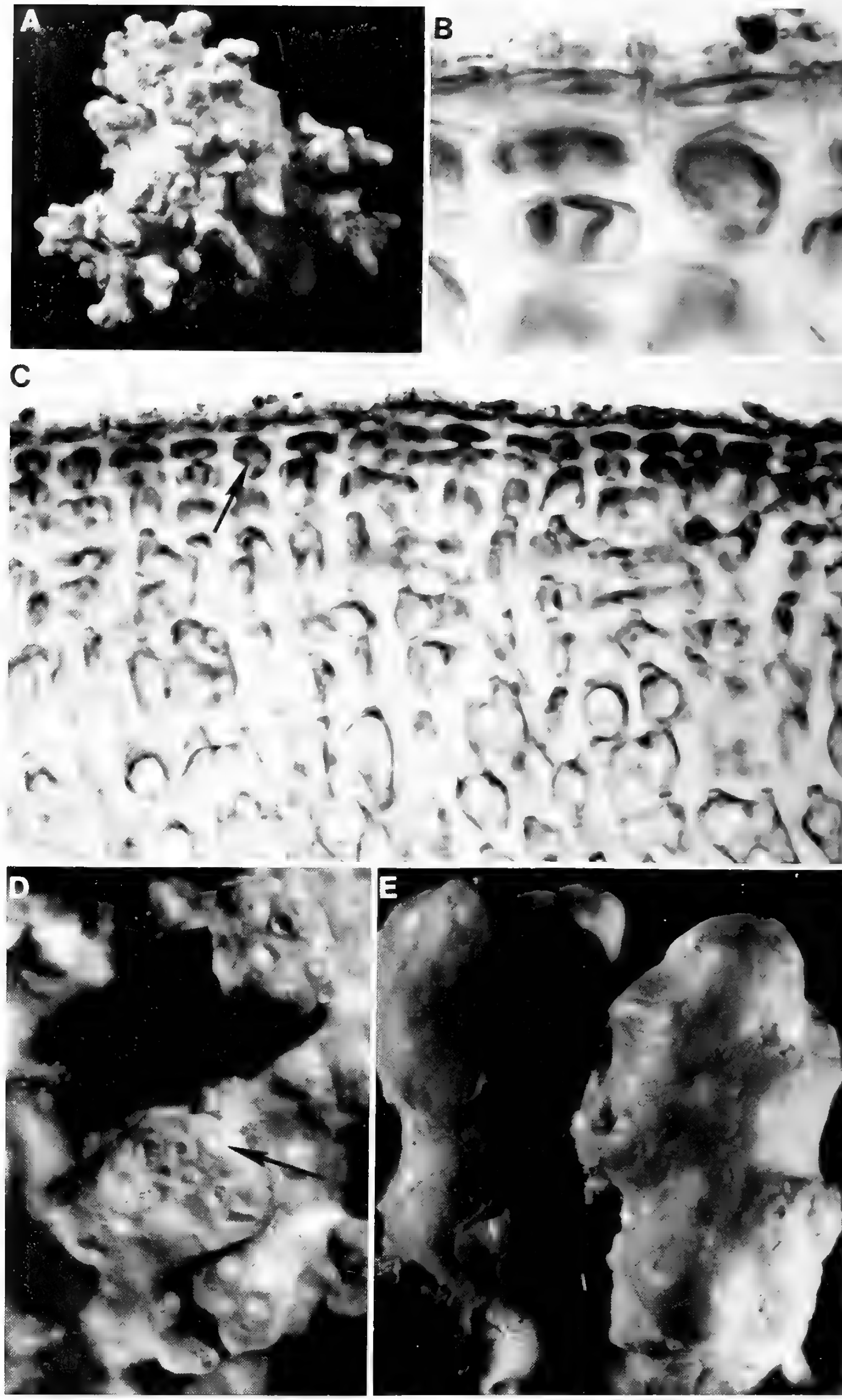


FIGURE 39.—*Lithothamnium australe:* A, habit, × 1; B, section through epithallium showing "*Lithothamnium*-type" cover cells, × 2200; C, section through thallus, note meristem (arrow) and perithallium, × 600; D, tetrasporangial conceptacles on surface of thallus (arrow), × 5; E, branch morphology, × 10. (Specimen nos.: A, D, E, 71-73; B, C, 71-72-1; micrographs reduced to 93%.)

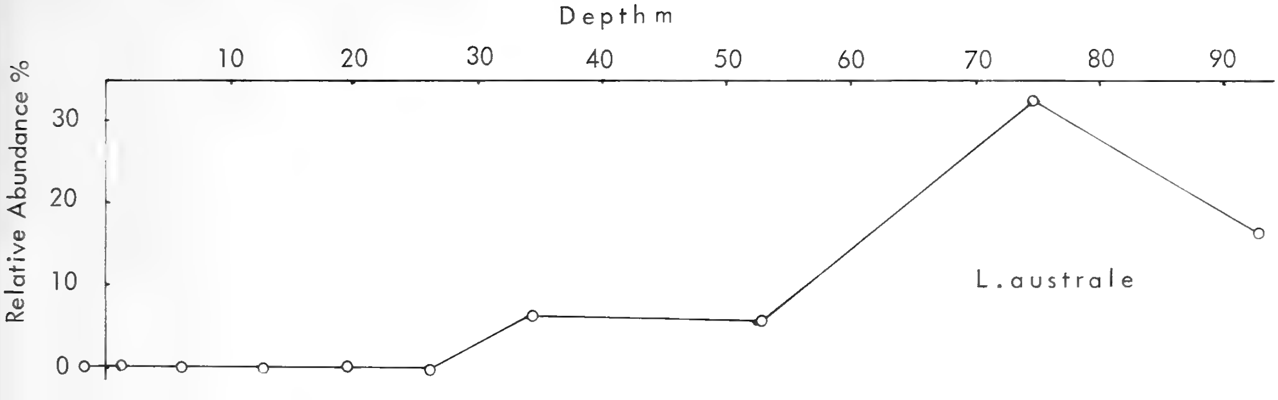


FIGURE 40.—Depth distribution of *Lithothamnium australe.*

topped multipored domes or conspicuous single-pored, pointed cones, often found on branch tips. Cover cells "*Lithothamnium*-type" (Figure 39B), single layer; cells 2–3 μm long and 3–12 μm diam. Intercalary meristem short and wide; cells 4–6 μm long and 5–10 μm diam. Perithallium multilayered, fusions frequent (Figure 39C), primary pit connections with darkly staining plugs; cells often becoming elongate with depth in tissue (Figure 37), 3–16 μm long and 3–11 μm diam. Hypothallium thin, parallel to substrate, 30–55 μm thick; cells 11–24 μm long and 4–10 μm diam. Tetrasporic conceptacles slightly raised, 300–500 μm O.D. (none seen in section). Male conceptacles unipored raised (50–150 μm), 300–450 μm O.D., 250–350 μm I.D., 90–110 μm high; spermatangial mother cells dendroid, restricted to floor of conceptacle cavity; spermatia discoid, 1–3 μm diam.

TYPE-LOCALITY.—Gulf of California: La Paz, Baja California del Sur.

LECTOTYPE.—Diguet (Foslie, 1895, fig. 7), in the herbarium of M. Foslie (TRH). Lecto-isotype: USNC.

DISTRIBUTION.—Borneo, Celebes, Gulf of California, Indian Ocean, Pacific Mexico, Panama, Philippines, Timor.

SPECIMENS STUDIED.—*Maui:* south-central, August 1971, 71-66-14, 71-67-16, 71-71-4. *Midway:* South Island, August 1971, 71-82-10. *Molakai:* south-central, August 1971, 71-69-7, 71-72-1, 71-72-2; southwest, August 1971, 71-73-35. *Oahu:* Waikiki, March 1971, 71-50-94.

REMARKS.—The typification of *Lithothamnium australe* is unclear from the literature. *Lithothamnium australe* was published as a nomen nudum in Foslie (1900c) (Taylor 1945). The name was first validly published by Foslie in Weber-van Bosse and Foslie (1904). As to the typification, Foslie states of *Lithothamnium australe* f. *americana*: "This form constitutes the basis of *Lithothamnion australe*. . . . The said form from the Gulf of California is here named f. *americana*" (Weber-van Bosse and Foslie 1904:25). The specimens from the Gulf of California are those collected by Diguet and given to Hariot, who sent them to Foslie. Foslie (1895) places these specimens under *Lithothamnium coralloides* P. & H. Crouan f. *australis* Foslie. It is misleading of Foslie to list as a synonym of *Lithothamnium australe* "*L. coralloides* f. *australis* Foslie Norw. Lith. p. 62, *ex parte*" (Weber-van Bosse and Foslie 1904:24), since he apparently did not wish to include any Norwegian material as types of *Lithothamnium australe.* It is also unfortunate that Foslie used as the species epithet the same name he had previously used as a forma name of a different taxon.

Since a holotype was not designated by Foslie (Weber-van Bosse and Foslie, 1904) and a lectotype has not been designated, we choose the specimen corresponding with Foslie (1895, fig. 7) as the lectotype of *Lithothamnium australe* Foslie.

Despite the "small-celled" meristem and progressive elongation of the perithallium (Figure 37) seen in this species, the cover cell shape is

characteristic of the genus *Lithothamnium*, and lacking reproductive details we have chosen to retain it in *Lithothamnium*.

Lithothamnium australe is the most abundant single species occurring in our collections from depths greater than 60 m (Figure 40). It was found throughout the Hawaiian chain wherever we dredged and occurred occasionally at 35 m, the limit of our diving range. It is abundant on bank situations as a small rhodolith or maerl-former and is the ecologic and anatomic "pair species" of the widespread Caribbean *Lithothamnium occidentale* (Foslie) Foslie.

Mesophyllum Lemoine, 1928

REMARKS.—*Mesophyllum* was the dominant genus on banks over 65 m and especially over 80 m. *Lithothamnium* followed close behind in abundance, with *Archaeolithothamnium* and finally *Hydrolithon* being lesser elements. Unlike the other genera, with one or two species each, *Mesophyllum* is represented by at least six species. We will describe and discuss the major elements, but considerable additional collecting preparation and study, especially in the central part of the Indo-Pacific, is necessary to satisfactorily accomplish a basic description of these bank floras.

Key to the Species of *Mesophyllum*

1. Branched (branches quickly developed from a crustose base) .... **M. madagascariensis**
   Crustose 2
2. Crusts extensive smooth, sub-leafy; conceptacles > 600 μm O.D. 3
   Crusts somewhat irregular; conceptacles < 600 μm O.D. 4
3. Few, scattered conceptacles, > 800 μm O.D. .... **M. prolifer**
   Densely concentrated mass of conceptacles, 600–800 μm O.D. .... **M. purpurascens**
4. Crusts irregular knobby, densely coated with raised conceptacles .... **M. syrphetodes,** new species
   Crusts not grossly irregular, conceptacles scattered .... **M. fluatum,** new species

Mesophyllum madagascariensis (Foslie) Adey

FIGURES 41A–C, 42

Mesophyllum madagascariensis (Foslie) Adey, 1970:25.
Lithothamnium erubescens Foslie f. *madagascariensis* Foslie, 1902b:3.—Masaki, 1968.
Lithothamnium madagascariensis Foslie, 1906:19.

DESCRIPTION.—Initially crustose plants yellowish pink to bluish pink in shaded areas, typically developing small dense finger-like or slightly flattened bifurcating branches, usually less than 2 mm diam. and 3 mm long, sometimes forming massive anastomosing branched growth (Figure 41A,B); large domed conceptables, more abundant in sparsely branched crusts. Epithallium single, rounded to quite angular; cells 2–4 μm long and 4–9 μm diam. Intercalary meristem elongate; cells oval, 4–10 μm long and 3–9 μm diam. Perithallium multilayered, thin when thallus crustose, staining bodies present, fusions frequent; cells 3–12 μm long and 3–9 μm diam. (Figure 42). Heterocysts abundant, single or in small groups, 7–19 μm long and 7–18 μm diam. Tetrasporangial conceptacles multipored, few initially raised (80 μm) but soon becoming buried, walls of sterile cells remaining (Figure 41c), 140–210 μm I.D., 60–90 μm high; tetrasporangia and bisporangia present, 60–90 μm long and 35–50 μm diam. Male conceptacles unipored (1 plant sectioned) 300–400 μm O.D., 140–208 μm I.D., 50–100 μm high; spermatangial mother cells simple, columnar, restricted to the conceptacle floor;

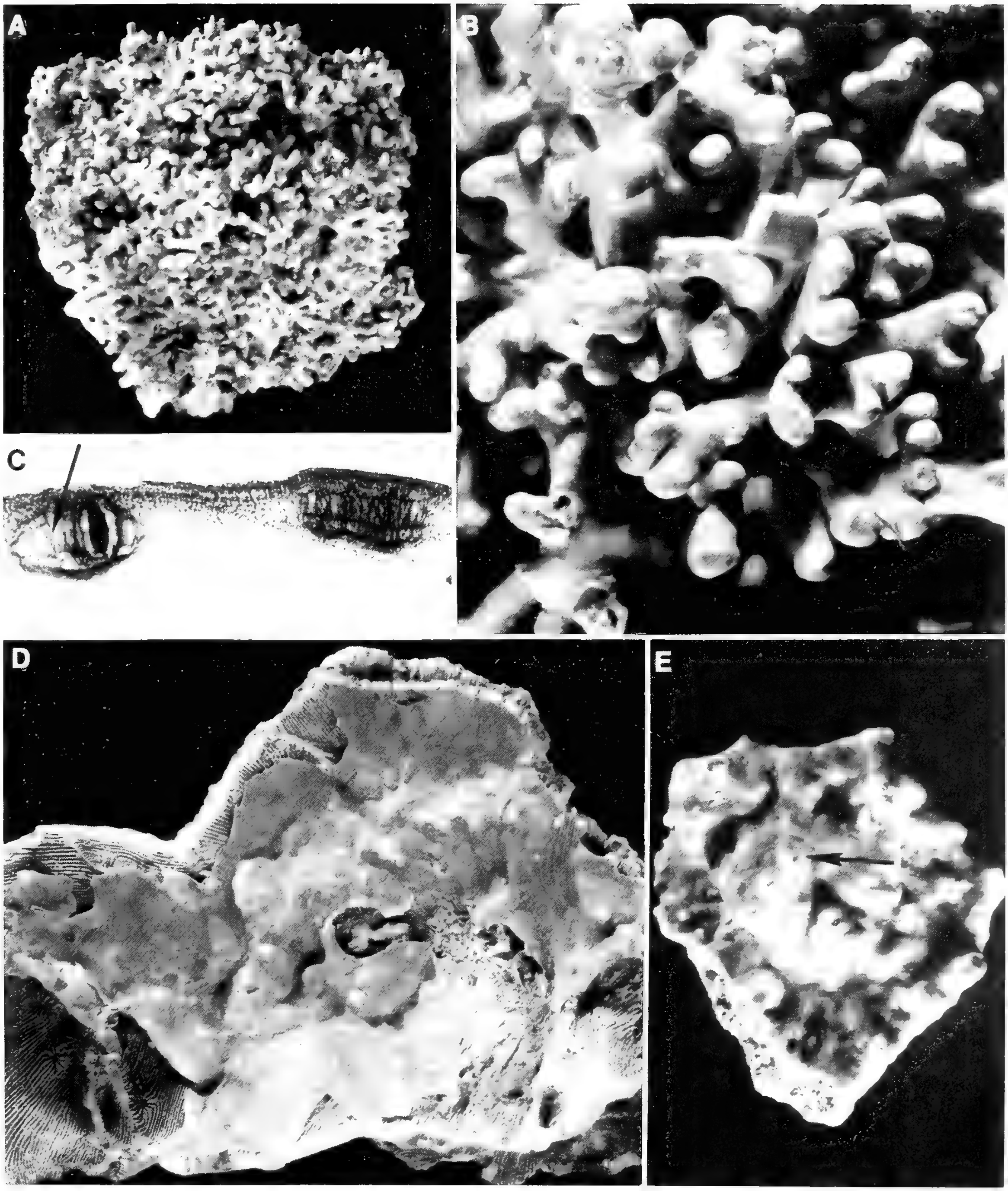


FIGURE 41.—*Mesophyllum madagascariensis:* A, habit of typical specimen, × 1; B, surface of thallus showing branches, × 5; C, section through tetrasporic plant, note sterile filaments in conceptacle cavity (arrow), × 100. *Mesophyllum prolifer:* D, habit of typical specimen, × 2; E, sexual conceptacles (arrow), × 5. (Specimen nos.: A, 71-81-35; B, 71-81-31; C, 71-81-9; D, 71-68-5; E, 71-70-(46).)

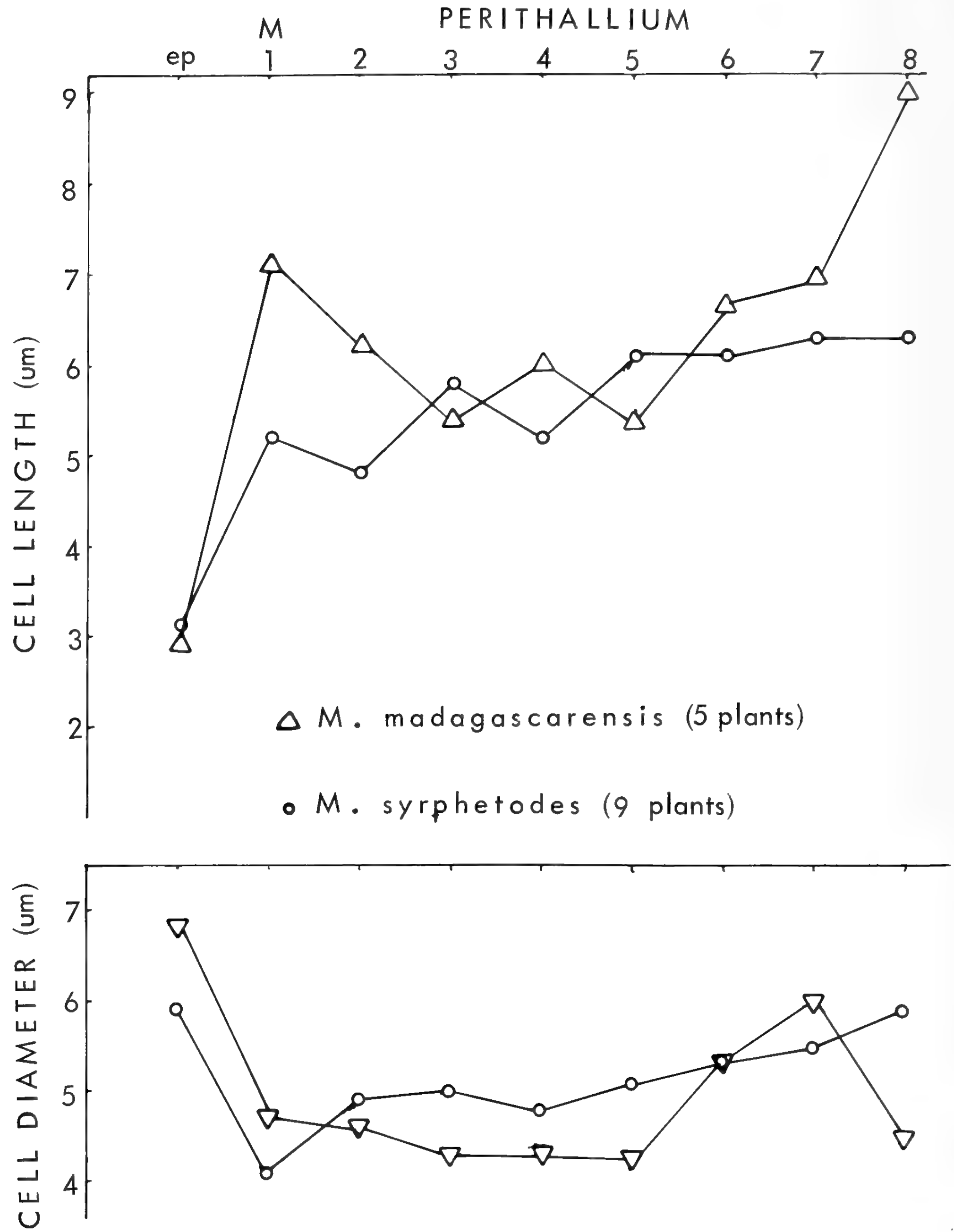


FIGURE 42.—Perithallial cell dimensions of *Mesophyllum madagascariensis* and *M. syrphetodes*, new species.

spermatia, ellipsoidal, in mucus strands, 2–3 μm long and 1–2 μm diam.

TYPE-LOCALITY.—Madagascar.

HOLOTYPE.—In herbarium of M. Foslie (TRH). Isotype: USNC.

DISTRIBUTION.—Ceylon, Madagascar, Japan.

SPECIMENS STUDIED.—*Hawaii:* Kawaihae, March 1971, 71–57–17. *Oahu:* Honauma, March 1971, 71-53-21; Kaneohe, August 1971, 71-81-9, 71-81-31, 71-81-35.

REMARKS.—Spermatangial mother cells in this species only occur on the floor of the conceptacle, not the roof and walls. This is at variance with the findings of Lebednik (1978) for *Mesophyllum*, although this is true for *Synarthrophyton patena* (Townsend, 1979).

Heterocysts are known in a few species of Melobesioideae (e.g., *Phymatolithon rugulosum*, Adey, 1964). They are known to the authors in a species of *Mesophyllum* important in southern Hokkaido, Japan, and have been reported from New Zealand (Johnson, pers. comm.) and Australia (R. Townsend). The plants we worked with in Hawaii are characterized by abundant single heterocysts.

Although this plant apparently occurs thoughout the Indo-Pacific and has a "pair species" (or possibly the same species, i.e., *Mesophyllum erubescens* (Foslie) Lemoine) in the tropical Atlantic, we encountered only a few large and and well-developed heads (about 15 cm diam.), and there is a total of only 10 specimens in our collection. Eight of the collected specimens came from the outer reef off Kaneohe Bay, Oahu, and all specimens were found from 3–12 m depth.

Mesophyllum prolifer (Foslie) Adey

FIGURE 41D,E

Mesophyllum prolifer (Foslie in Weber-van Bosse & Foslie) Adey, 1970:25.
Lithothamnium prolifer Foslie in Weber-van Bosse & Foslie, 1904:18.

DESCRIPTION.—Thin, dark pink somewhat leafy crust, surface usually nonlustrous, undulate, sometimes developing random low knobs (Figure 41D). Epithallium single layer of rounded cells, 3–4 μm long and 4–7 μm diam. Intercalary meristem elongate; cells 4–5 μm long and 5–6 μm diam. Perithallium multilayered, irregular; cells somewhat square, 2–10 μm long and 3–9 μm diam. Hypothallium weakly coaxial 20–60 μm thick; cells 7–27 μm long and 5–12 μm diam. Tetrasporangial conceptacles multipored, low and rounded domes, epithallium persistent, 800–1200 μm O.D. (none sectioned). Sexual conceptacles single pored sharply raised (Figure 41E), none sectioned.

TYPE-LOCALITY.—Pulu Sebangkatan, Borneo Bank, Borneo; 34 m depth, coral bottom and *Lithothamnium.*

LECTOTYPE.—Weber-van Bosse, 971, 14 June 1899, in herbarium of M. Foslie (TRH) (Adey, 1970).

DISTRIBUTION.—Borneo.

SPECIMENS STUDIED.—*Maui:* South-central, August 1971, 71-68-5, 71-70-(46).

REMARKS.—Only six specimens of this plant occur in the collection, all from about 80 m on the bank on the lee side of Maui. A presently unnamed "pair species," quite similar in anatomy and morphology, is known to the authors from deep reef situations in the Caribbean.

Mesophyllum purpurascens (Foslie) Adey

FIGURE 43

Mesophyllum purpurascens (Foslie) Adey, 1970:26.
Lithothamnium funafutiense Foslie f. *purpurascens* Foslie, 1901b:18.
Lithothamnium purpurascens Foslie, 1907a:182; 1929.—Lemoine, 1917; 1965.—Papenfuss, 1968.

DESCRIPTION.—Crusts smooth thin and glossy (Figure 43A). Epithallium a single layer of rounded cells, 2–3 μm long and 5–8 μm diam. Intercalary meristem elongate; cells 6–8 μm long and 4–6 μm diam. Perithallium multilayered, zoned from formation of conceptacles; cells 4–8 μm long and 3–6 μm diam. (Figure 43B). Hypothallium multilayered, coaxial; cells 10–16 μm long and 3-4 μm diam. (Figure 43E). Tetrasporangial conceptacles centrally crowded (Figure 43A), raised (150 μm) (Figure 43D), becoming buried (Figure 43B), 500–900 μm O.D., 300–700 μm I.D., 180–270 μm high, walls of sterile cells remaining in cavity (Figure 43B,C); tetrasporangia not seen.

TYPE-LOCALITY.—Koh Mesan and Cape Liant, Gulf of Thailand, 18 m depth.

LECTOTYPE.—Danish expedition to Thailand,

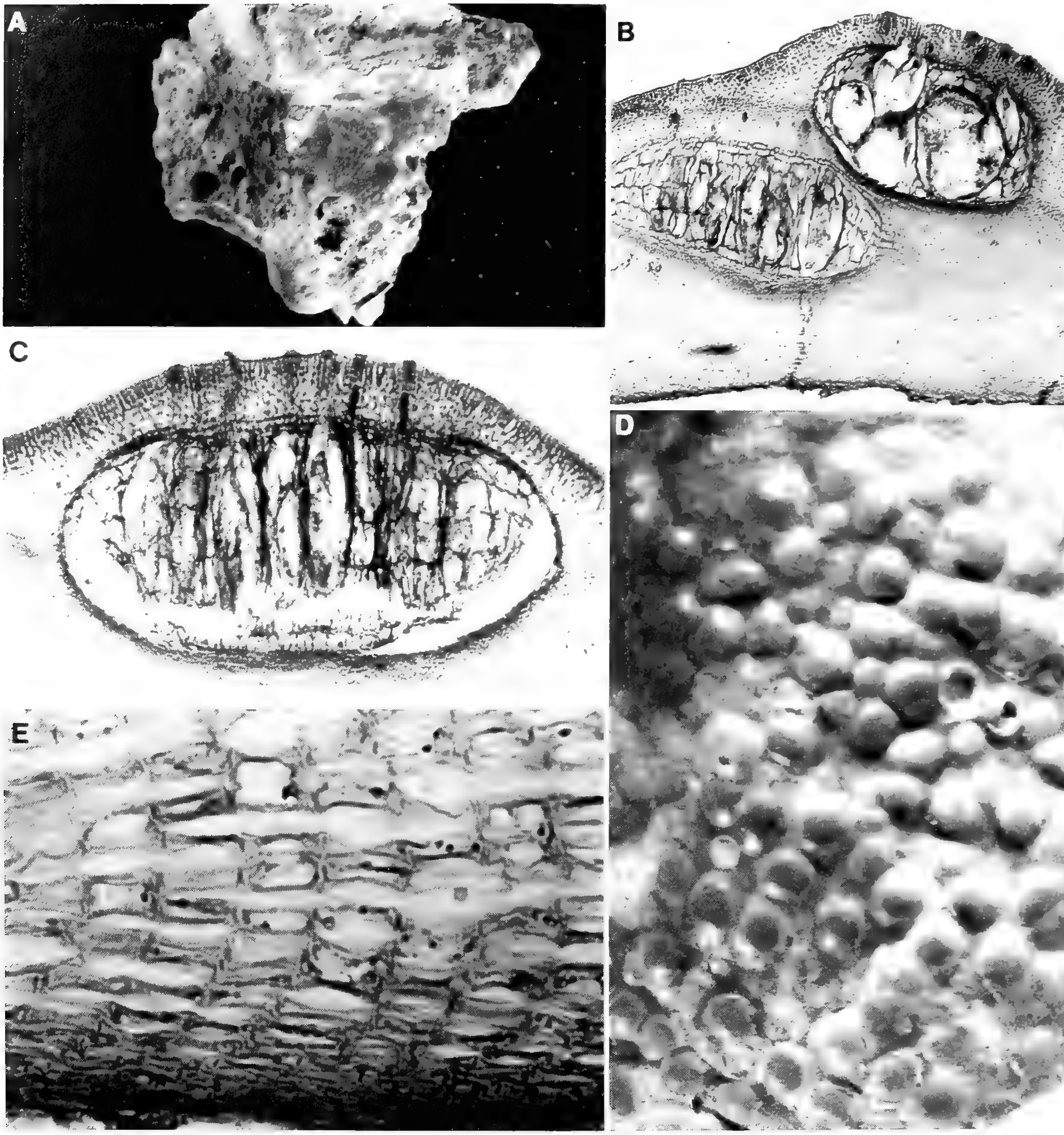


FIGURE 43.—*Mesophyllum purpurascens:* A, habit showing centrally placed tetrasporangial conceptacles, × 1; B, section through tetrasporangial thallus showing buried conceptacle, × 150; C, section through tetrasporangial conceptacle, × 300; D, surface view of tetrasporangial conceptacles, × 20; E, coaxial hypothallium, × 1000. (Specimen nos.: A–E, 71-66-2.)

1900, in herbarium of M. Foslie (TRH). Lectoisotype: USNC.

DISTRIBUTION.—Indian Ocean, Red Sea, Thailand.

SPECIMENS STUDIED.—*Maui:* south-central, August 1971, 71-66-2; 71-67-3.

REMARKS.—Only two specimens of this species were found in this study. A morphological and ecological "pair species" of this species has not been found in the Caribbean.

Mesophyllum syrphetodes, new species

FIGURES 42, 44

DESCRIPTION.—Crustae prinum tenues rosaceae, superficie sordida, margines supercrescentes interdum abundantes, quam ob rem crusta usque ad plura mm. crassitudine facta (Figura 44A,C). Epithallium 1–2 cellulis crassum, cellula exteriore cellulam-obtegentem interdum efficiente; cellulae rotundatae 2–4 μm long. atque 4–8 μm diam. Meristema intercalare non manifeste elongatum; cellulis 3–7 μm long. atque 3–5 μm diam. Perithallium pluristratosum, tenue, ordinationem inconspicue zonatam praebens, praecipue regionibus auctus conceptaculorum, et fusionibus non frequentibus, una heterocysta visa; cellulae rotundatae, 3–9 μm long. atque 3–8 μm diam. (Figurae 44C, 42). Hypothallium pluristratosum, parallelum ad coaxiale, 20–75 μm crass.; cellulae 10–20 μm long., 5–9 μm diam. Conceptacula tetrasporangialia multiporata, crebre disposita (Figura 44B) in quibusdam plantae regionibus repetite evenientia, frequenter obtecta facta et crassitudinem plantae augentia (Figura 44C), elevata (80–180 μm), tholiformia (Figura 44B,C), 250–400 μm O.D., 150–300 μm I.D., 70–120 μm alt.; tetrasporangia 80–90 μm long. atque 25–45 μm diam.

Initially thin, reddish pink crusts with a dull surface, sometimes overgrowing margins abundant and crust achieving many mm of thickness by overgrowing (Figure 44A,C). Epithallium 1–2 cells thick, outer cell may form cover cell; cells rounded, 2–4 μm long and 4–8 μm diam. Intercalary meristem not markedly elongate; cells 3–7 μm long and 3–5 μm diam. Perithallium multilayered, thin with faint zonate pattern, especially in areas of conceptacle development, and fusions not common, one heterocyst seen; cells rounded 3–9 μm long and 3–8 μm diam. (Figures 44C, 42). Hypothallium multilayered, parallel to coaxial, 20–75 μm thick; cells 10–20 μm long 5–9 μm diam. Tetrasporangial conceptacles multipored, densely spaced, (Figure 44B) occurring repeatedly in certain areas of the plant, frequently becoming overgrown and adding to thickness of plant (Figure 44C), raised (80–180 μm), domed (Figure 44B, C), 250–400 μm O.D., 150–300 μm I.D., 70–120 μm high; tetrasporangia 80–90 μm long and 25–45 μm diam., bisporangia present (Figure 44C). Sexual plants not seen.

TYPE-LOCALITY.—Southwest Molokai, Hawaii (21°0′N, 157°0′W), 70 m depth.

HOLOTYPE.—D. Child, 71-72-2, August 1971 (USNC), Figure 44A.

PARATYPES.—*Maui:* south-central, August 1971, 71-71-1. *Molokai:* southwest, August 1971, 71-65-1, 71-73-6. *Midway:* South Island, August 1971, 71-82-20. *Oahu:* Kaneohe, August 1971, 71-81-15.

DISTRIBUTION.—Throughout the archipelago.

REMARKS.—The specific epithet *syrphetodes* refers to the appearance of the thallus.

A morphological and ecological "pair species" of this species has not been found in the Caribbean.

Mesophyllum fluatum, new species

FIGURE 45

DESCRIPTION.—Crustae tenues rosaceae (25–100 μm), super superficiem "profluens," et non praesertim rugatae neque substratum plane illustrantes (Figura 45A,B). Epithallium ex unico strato cellularum rotundatarum, 3–4 μm long. atque 3–5 μm diam. constans. Meristema intercalare non elongatum, cellulis 2–6 μm long. atque 4–7 μm diam. Perithallium pluristratosum, cellulis 4–7 μm long. atque 4–12 μm diam. Hypothallium pluristratosum coaxiale, 20–25 μm crass.; cellulis 10–17 μm long. atque 4–5 μm crass.

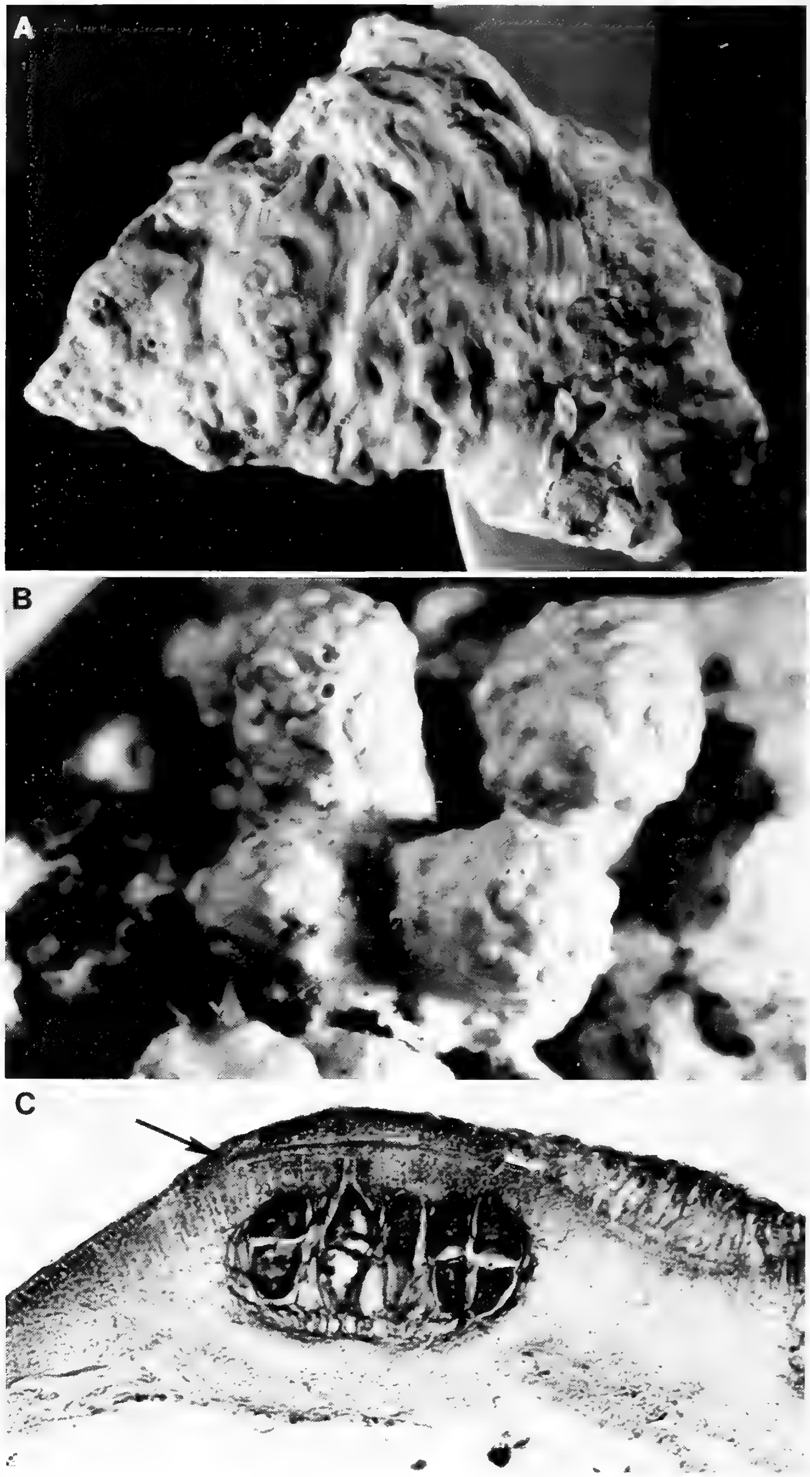


FIGURE 44.—*Mesophyllum syrphetodes*, new species: A, habit of type specimen, × 2; B, surface morphology of bisporangial plant, × 10; C, section through thallus, note overgrowing (arrow), × 200. (Specimen nos.: A, 71-72-2; B, C, 71-73-6; micrographs reduced to 92%.)

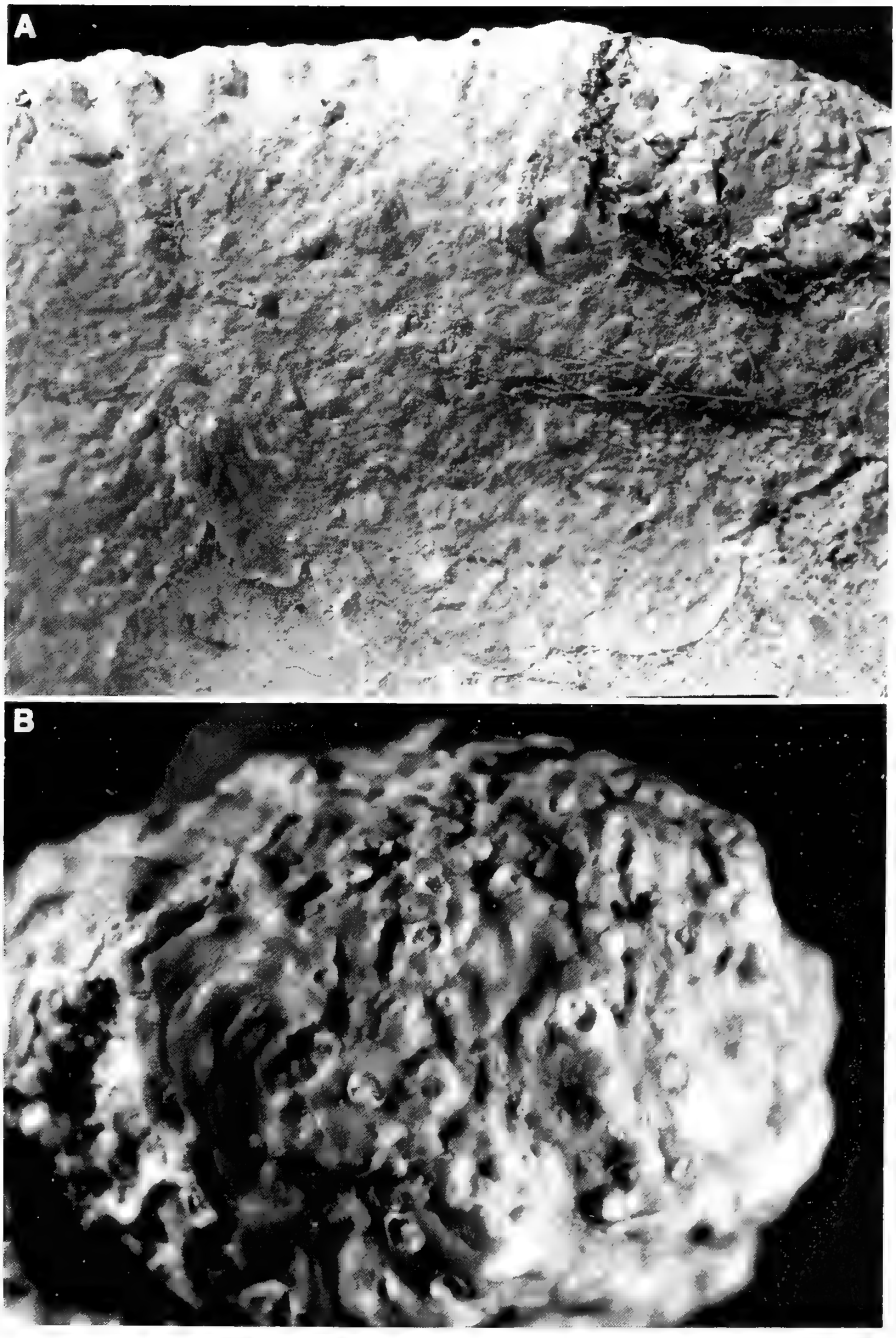


FIGURE 45.—*Mesophyllum fluatum*, new species: A, habit of type specimen, × 2; B, surface morphology of typical specimen, note tetrasporangial conceptacles (arrow) and conceptacle scars (arrowhead), × 150. (Specimen nos.: A, B, 71-68-2.)

Conceptacula tetrasporangialia multiporata, super superficiem dispersa (Figura 45B), elevata (50–100 μm) 300–500 μm O.D. (solum a superficie visa). Conceptacula carposporangialia uniporata, (solo uno secto) 525 μm O.D., 350 μm I.D., 150 μm alt.; carposporangia ad periferiam conceptaculi restricta; sporangia 45–50 μm long. atque 60–75 μm diam.; cellula-coalescens reticulata.

Thin pink crusts (25–100 μm), "flowing" over the surface and not particularly crumpled or strongly reflecting the substrate (Figure 45A,B). Epithallium single layer of rounded cells, 3–4 μm long and 3–5 μm diam. Intercalary meristem not elongate; cells 2–6 μm long and 4–7 μm diam. Perithallium, multilayered; cells 4–7 μm long and 4–12 μm diam. Hypothallium multilayered coaxial, 20–25 μm thick; cells 10–17 μm long and 4–5 μm diam. Tetrasporangial conceptacles multipored, scattered over surface (Figure 45B), raised (50–100 μm), 300–500 μm O.D. (only seen from surface). Carposporangial conceptacles unipored, (only 1 sectioned) 525 μm O.D., 350 μm I.D., 150 μm high; carposporangia restricted to the conceptacle periphery; sporangia 45–50 μm long and 60–75 μm diam.; fusion cell reticulate.

TYPE-LOCALITY.—South-central Maui-Hawaii, 92 m.

HOLOTYPE.—D. Child, 71-68-2, August 1971 (USNC), Figure 45A.

PARATYPES.—*Maui:* south-central, August 1971, 71-70-6. *Molokai:* southwest, August 1971, 71-68-13. *Nihoa:* West, August 1971, 71–75.

DISTRIBUTION.—Throughout south and central archipelago.

REMARKS.—The specific epithet *fluatum* refers to the "flowing" of the crust over the substrate. *Mesophyllum fluatum* is represented in the collection by 11 specimens. All of these were collected from 60–90 m depth. No Caribbean "pair species" is known to exist for *M. fluatum.*

Discussion

Figure 46 compares the patterns of generic depth distribution in the eastern Caribbean area and the Hawaiian Archipelago. Considerable correlation can be seen in the major characteristics of generic dominance: *Porolithon* and *Neogoniolithon* dominate between intertidal to over ~ 30 m; *Lithothamnium*, *Mesophyllum*, and *Archaeolithothamnium* dominate at depths greater than 50 m. This correlation, along with the large number of pair species generally having similar spatial ecologies, indicates that crustose coralline evolution has been very slow since the Indo-Pacific and the Caribbean were separated in the Miocene. The possibility of detailed interpretation of Neogene paleoecology, by using the relative abundance of genera found in limestone cores and outcrops, becomes apparent.

Considerable detail in environmental interpretation can be gained using only the easily recognizable generic characteristics that often occur in well-preserved coralline fossils, especially type and placement of heterocyst fields, type of hypothallium, and the presence of sporangial sori and multipored conceptacles. Occasionally even more precise determination is possible with the occurrence of certain distinctive species that have clearly defined ecological niches. For instance, *Porolithon onkodes* becomes dominant and forms thick crusts only on the shallowest wave-beaten outer and upper faces of algal ridges and coral reefs. This species is easily separated from the profusely branched *P. gardinerii*, the only other member of the genus found in the area.

Reef-flat areas, although as shallow as the range dominated by *Porolithon onkodes*, seldom have appreciable amounts of that species. Such flats are often characterized by a red boring algae (melobesioid "C" of Littler, 1973A), which is probably a destructive rather than constructive agent. Crustose corallines are present usually on the shaded sides and undersides of rubble, the most common species being *Hydrolithon reinboldii* and the easily distinguishable *Archaeolithothamnium erythraeum.* These species are very useful as ecological indicators; both are sharply restricted to shallow water and have distinguishing morphological characteristics making easy identification possible. The large cells of *H. reinboldii* set if off from the other species of the genus (Figure 15); the unique sori of *Archaeolithothamnium* should easily be seen in fossilized material, and the difference in their relative size is often great enough to distinguish *A. erythraeum* from *A. episoredion*—the latter is consistently associated with deeper water. The presence of abundant *Hydrolithon* and *Archaeolithothamnium* in a geological sample, even if not determinable to species, would suggest shaded

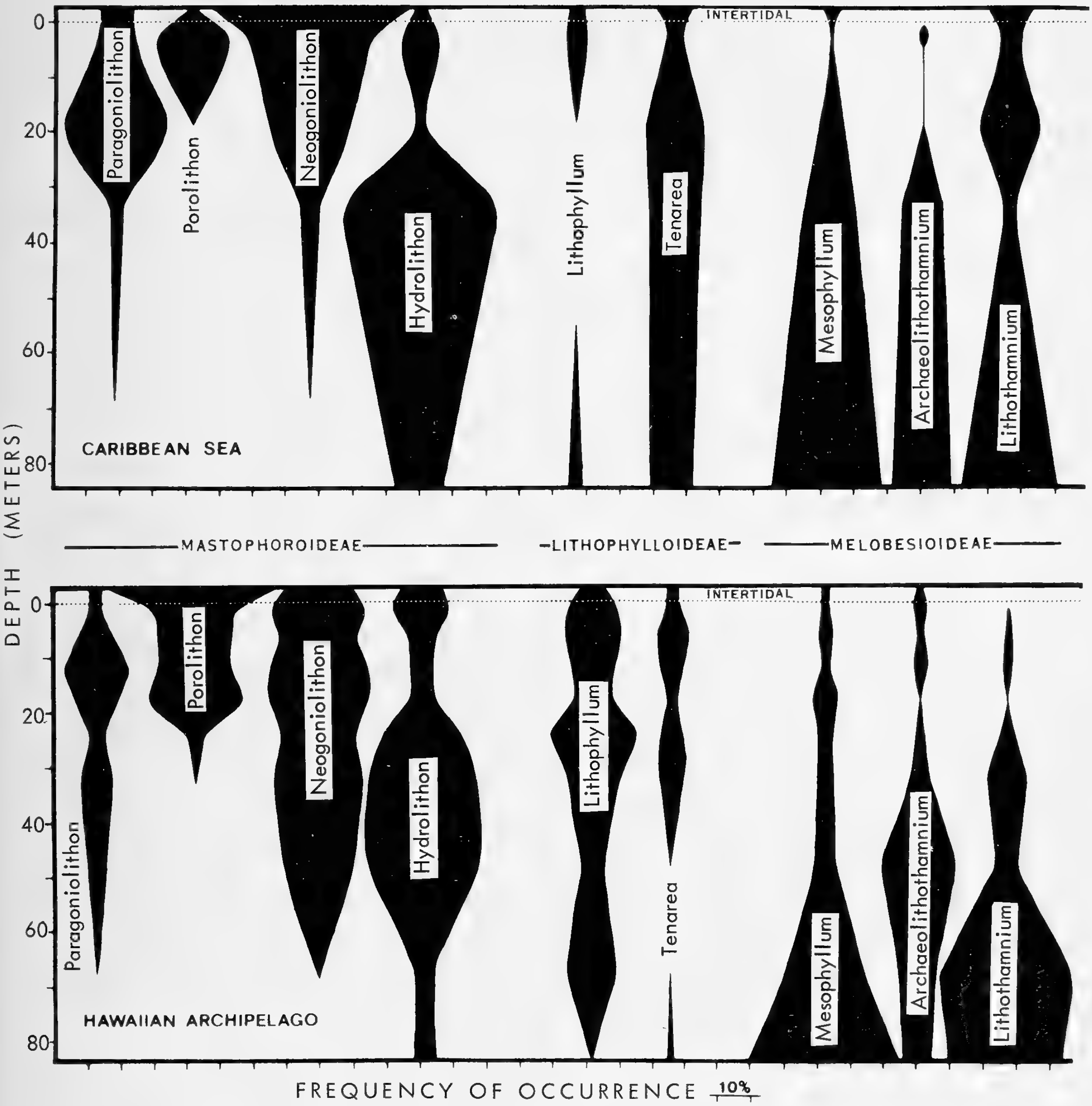


FIGURE 46.—Comparison of distribution patterns of crustose coralline genera (except *Lithoporella*) in idealized littoral zones in the Hawaiian Islands and Caribbean.

reef flat environments only if *Lithothamnium* and *Mesophyllum* species were not present. Doty (1974) reports abundant *Hydrolithon* and *Archaeolithothamnium* from the reef crest, but they were not found in that position in this study. On more protected reef flats and in shallow lagoons, the elongate and slender type of branching seen in *Porolithon gardinerii* and *Neogoniolithon frutescens* may be encountered. It is not likely that either of these would be found outside the reef and at any great

depth. It is possible to find representatives of species characteristic of much deeper water in shallow areas, but these occurrences are limited to cryptic situations where light conditions are similar to those existing at depth.

Abundant coarsely branched *Hydrolithon*, if mixed with a branching *Lithophyllum*, would indicate deeper fore-reefs or island slopes (15–20 m). Large amounts of *Lithothamnium* and *Mesophyllum*, especially if in rhodolith (nodule) form, can only indicate bank depths of greater than 50–60 m. Although members of both of these genera do not occur in shallow water, they are not nodule formers in these environments but are represented by thin crusts in cryptic reef and ridge environments. Shade-loving *Neogoniolithon* species usually dominate in those areas.

Glossary

Branch. Outgrowth of plant in which the height above the thallus surface is greater than the largest diameter of the growth (Figure 17C).

Columella. One of several paraphyses situated directly below the pore in a uniporate tetrasporangial conceptacle (Figures 6E, 24E).

Coralgal. A calcareous substrate consisting of coral and corallines or other calcareous algae.

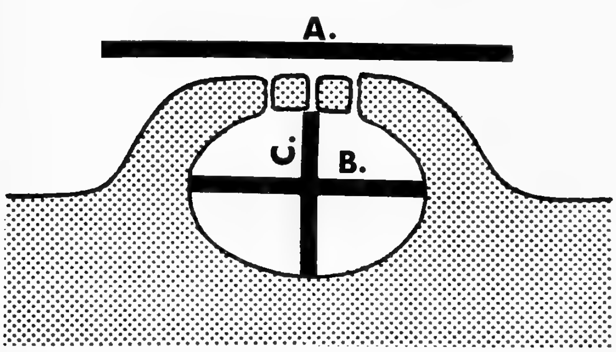


FIGURE 47.—Schematic representation of the conceptacle.

Cover cell. More or less specialized cells (e.g., thick walls), which form the outer layer of epithallium and form a protective layer over the surface of the thallus (Figures 18C, 29D, 13C).

——— "*Lithothamnium*-type" cover cells. Characteristic of *Lithothamnium* (Figure 31C, D).

High (conceptacle). Measurement C, Figure 47.

I.D. (inside diameter, conceptacle). Internal widest diameter of a conceptacle when sectioned through the true median plane, measurement B, Figure 47.

Intercalary meristem. Layer of meristematic cells giving rise to the epithallium in one direction and the perithallium in the other direction (Figures 18C, 29D).

Layered (perithallium). Tissue whose cells form regular horizontal rows (Figures 24F, 27C).

Leafy. Crust that is partially loose, especially at the growing margins, and appearing as a "leaf" upon the substrate.

Mammillon. Outgrowth of the crust in which the height above the thallus surface is less than the largest diameter of the structure (Figure 17A,B).

O.D. (outside diameter, conceptacle). External widest diameter of a conceptacle when viewed from the surface, measurement A, Figure 47.

Parallel (hypothallium). Tissue where the filaments run in line with the substrate and are not coaxial. See "Simple" (Figure 8B).

Pair species. Similar taxa separated by land masses or other barriers. The taxa exhibit similar morphology (morphological p.s.) and/or exist in similar niches (ecological p.s.).

Plumose (hypothallium). Ascending and descending filaments from a single-or few-layered central plane, which give the hypothallium the look of a fountain in section (Figure 2F).

Rugose (surface). A surface with an irregular low-mounded appearance as though covered with wrinkles, not corrugations as Foslie (1906) used for *Porolithon antillarum* (Foslie & Howe) Foslie.

Rugulose (surface). Diminutive of rugose.

Simple (hypothallium). Noncoaxial.

Spermatangial mother cell. Cell giving rise to spermatia.

Tessellate (surface). Mosaic surface of irregular patterns, sometimes polygonal, not the spiral whirls of *Tenarea tesselatum* that Lemoine (1929) incorrectly considered tesselate (cf. to surface of *Hydrolithon reinboldii*).

Zonate, zoned (perithallium). Tissue with large scale (as opposed to cellular) layering or other patterning (Figure 12C).

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